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FACTORS CONTROLLING THE DISTRIBUTION OF DESICCATION-TOLERANT PLANTS IN WEST AFRICA

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DEDICATION

*I dedicate this thesis to my beloved parents, **Fatima IDE** and **Ibrahim SEIDOU**, whose unwavering guidance, patience, encouragement, and unconditional support have sustained me throughout this academic journey and shaped both my educational path and personal growth. Their love and prayers have been my greatest source of strength during the years of study and research that led to this work.*

~~~

## FOREWORD

This thesis was conducted as part of my PhD research and focuses on the ecology, distribution, and conservation of desiccation-tolerant vascular plants in West Africa. My interest in this topic developed during my academic training and emerged from a growing awareness of the accelerating global loss of biodiversity. This loss is driven largely by the increasing impacts of climate change, particularly in regions where water availability is a major limiting factor for plant survival, as well as by the uneven attention given to different groups of organisms in conservation research and practice. While much emphasis has been placed on forest ecosystems and economically important species, other biologically remarkable yet less conspicuous taxa remain largely overlooked. Desiccation-tolerant plants, despite their exceptional physiological ability to survive extreme drought and their potential ecological and applied value, are among these neglected groups, particularly in regions such as West Africa, where they remain poorly documented. This research aims to provide a better understanding of desiccation-tolerant plants and the drivers that influence their current and future geographical distribution in West Africa by combining species occurrence data, species distribution modeling, and climate-based drought indices.

Conducting this research provided an opportunity to engage with questions at the intersection of biogeography, ecology, and pressing conservation challenges, while addressing knowledge gaps that are especially pronounced in this part of the world. West Africa represents a particularly compelling context for this work, as it combines strong climatic gradients with increasing land-use pressures. Through this work, I sought to better understand how large-scale drivers such as climate change, as well as local factors including soil variability and life-history traits, shape the distribution, ecological strategies, and persistence of desiccation-tolerant plants.

This thesis integrates multiple approaches, ranging from literature synthesis and spatial analyses to field-based ecological measurements and experimental work. Together, these approaches provide a comprehensive framework for assessing how climate change and other factors may affect the distribution, diversity, and exposure of desiccation-tolerant plants across West Africa. The research process involved challenges related to data availability, field logistics, and working across different spatial and biological scales. Overcoming these challenges was an important part of my academic training and contributed significantly to my development as a researcher.



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## LIST OF ABBREVIATIONS AND ACRONYMS

**AUC:** Area under the receiver operating characteristic

**Ca50:** Circular Area with a radius of 50 km

**CMIP6:** Coupled Model Intercomparison Project

**CSR:** competitiveness, ruderalism, and stress-tolerance

**DT plants:** Desiccation-tolerant vascular plants

**GBIF:** Global Biodiversity Information Facility

**GCM:** Global Climate Model

**GHG:** Greenhouse Gas

**IDW:** Inverse-distance weighted model

**IPCC:** Intergovernmental Panel on Climate Change

**IUCN:** International Union for Conservation of Nature

**LA:** Leaf area

**LDMC:** Leaf dry matter content

**MaxEnt:** Maximum entropy

**POWO:** Plants of the World Online

**RCP:** Representative Concentration Pathways

**SLA:** Specific leaf area

**SPEI:** Standardized Precipitation Evapotranspiration Index

**SSP:** Socioeconomic Pathways

**SRES:** Special Report on Emission Scenarios

**TSS:** True Skills Statistic

**UNFCCC:** United Nations Framework Convention on Climate Change

**AR:** Assessment Report

**WMO:** World Meteorological Organization

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## ABSTRACT

Biodiversity loss driven by human activities is accelerating globally, yet some functional groups remain largely overlooked in conservation planning. Desiccation-tolerant (DT) vascular plants, which can survive extreme dehydration, are among these overlooked taxa and face increasing threats from climate change and anthropogenic pressures. This thesis provides the first comprehensive assessment of desiccation-tolerant vascular plants in West Africa, a region of high biodiversity value and growing vulnerability to land-use change and climate extremes, addressing knowledge gaps in their diversity, distribution, ecological strategies, and conservation needs under global change. First, we compiled a checklist of DT species in the region, systematically reviewed the literature on their conservation status, and evaluated their representation in protected areas relative to anthropogenic threats such as quarrying and climate change. The results of this work show that only 14% of species have been assessed by the IUCN, and conservation needs are rarely discussed in the existing literature. Notably, the species that are the most exposed to threats were also the least represented in protected areas, which proved more effective at reducing quarrying impacts than at mitigating climate change. Second, species distribution models were used under current and projected climate scenarios, and the findings reveal a substantial contraction of distribution ranges, an increased fragmentation, and a significant reduction in species diversity and endemism centers. The findings highlighted the vulnerability of desiccation-tolerant plants to future climate conditions and the need to integrate climate-informed strategies into conservation planning. Third, the role of soil was explored in shaping intraspecific variation in ecological strategies among four selected desiccation-tolerant grasses. Although there are no significant relationships between soil variables and CSR strategies detected, the predominance of stress-tolerant strategies suggests an overriding influence of disturbance or other environmental drivers. Finally, experimental results demonstrated that seed age may compromise early seedling desiccation tolerance, revealing critical vulnerabilities during early life stages. This study stresses the urgent need to integrate desiccation-tolerant plants into biodiversity conservation frameworks through mechanistic, climate-informed approaches that account for species vulnerability in terms of exposure, sensitivity, and adaptive capacity. By combining ecological, physiological, and biogeographic perspectives, this work establishes a foundation for prioritizing desiccation-tolerant plants in conservation planning and provides actionable insights to enhance species persistence under increasingly water-limited conditions and the broader challenges of global change.

**Keywords:** Climate change; Conservation; Desiccation tolerance; Diversity; Endemism; Resurrection plants, land use change; protection areas; quarrying; rock outcrops, CSR strategy

## RÉSUMÉ

La perte de biodiversité due aux activités humaines s'accélère à l'échelle mondiale, mais certains groupes fonctionnels demeurent largement négligés dans la planification de la conservation. Les plantes vasculaires tolérantes à la dessiccation, capables de survivre à une déshydratation extrême, figurent parmi ces taxons négligés et font face à des menaces croissantes liées au changement climatique et aux pressions anthropiques. Ce travail fournit la première évaluation des plantes vasculaires tolérantes à la dessiccation en Afrique de l'Ouest, tout en comblant des lacunes dans les connaissances sur leur diversité, leur distribution, leurs stratégies écologiques et leurs besoins en matière de conservation dans un contexte de changement global. D'abord, une revue systématique de la littérature a été faite afin de dresser la liste des plantes tolérantes à la dessiccation présentes en Afrique de l'ouest et d'évaluer leur statut de conservation. Les résultats montrent que seulement 14 % des espèces ont été évaluées par l'UICN et que les besoins en conservation sont rarement abordés dans les études existantes. Notamment, les espèces les plus exposées aux menaces sont aussi celles qui sont les moins représentées dans les aires protégées, lesquelles s'avèrent être plus efficaces pour réduire les impacts liés aux carrières minières que ceux du changement climatique. Ensuite, nous avons utilisé des modèles de distribution des espèces sous les scénarios climatiques actuels et futurs. Les résultats ont révélé une contraction substantielle des aires de répartition et une fragmentation accrue des centres de diversité et d'endémisme, montrant ainsi la vulnérabilité de ces plantes face aux conditions climatiques futures. Aussi, le rôle du sol a été exploré dans la variation des stratégies écologiques chez quatre graminées tolérantes à la dessiccation. Bien qu'aucune relation significative entre les variables du sol et les stratégies CSR n'ait été détectée, la prédominance des stratégies tolérantes au stress suggère une influence des perturbations ou d'autres facteurs environnementaux. Enfin, des expériences ont montré que l'âge des graines pourrait compromettre la tolérance à la dessiccation des jeunes plantules avec des vulnérabilités critiques aux premiers stades de leur développement. Ce travail souligne l'urgence d'intégrer les plantes tolérantes à la dessiccation dans le cadre de la conservation tout en prenant en compte la vulnérabilité des espèces en termes d'exposition, de sensibilité et de capacité d'adaptation. En combinant des perspectives écologiques, physiologiques et biogéographiques, ce travail établit une base pour la priorisation de ces espèces dans la planification de la conservation et fournit des recommandations concrètes afin de renforcer leur persistance face aux défis globaux.

**Mots-clés:** Changement climatique; Conservation; Tolérance à la dessiccation; Diversité; Endémisme; Plante de résurrection; Changement d'usage des terres; Aires protégées; Extraction de carrières; Affleurements rocheux; Stratégie CSR.



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## **INTRODUCTION**

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The world is experiencing unprecedented rates of biodiversity loss driven by human activities **(Sinclair, 2000; Bergès *et al.*, 2010; Jaureguiberry *et al.*, 2022)**. Developing global strategies for biodiversity conservation remains challenging because anthropogenic drivers of biodiversity loss operate in diverse ways and species are often exposed to multiple stressors simultaneously **(Sinclair, 2000; Bellard *et al.*, 2022)**. Land-use change typically results from direct and local interventions in natural systems, whereas climate change arises from global human activities and affects regions differently regardless of their contribution to its causes **(Chaplin-Kramer *et al.*, 2019)**. The intensity of both land use change and climate change is rising in some regions of the world, such as West Africa **(Venter *et al.*, 2016; WMO, 2024)**, which includes areas recognized as global biodiversity hotspots **(Myers *et al.*, 2000)**. The combined effects of these drivers amplify human pressures on species and their habitats, making the need for effective conservation strategies much more urgent. However, certain groups of species remain largely neglected in conservation planning. Given the limited resources available, identifying species or regions most at risk is essential for safeguarding biodiversity efficiently **(Cullen, 2013)**.

Desiccation-tolerant (DT) vascular plants are a striking example of such neglected taxa. These plants form a paraphyletic group, also known as “resurrection plants” or “poikilohydrous” species, with the remarkable ability to survive the loss of up to 95% of their water content (equivalent to 0.1 g H<sub>2</sub>O/g dry weight) and resume metabolism upon rehydration with minimal or no biomass loss **(Porembski and Barthlott, 2000; Marks *et al.*, 2021; Marks *et al.*, 2025)**. This ability is expected to provide an ecological advantage to thrive in environments such as inselbergs and ferricretes, which experience frequent droughts events throughout the year **(Marks *et al.*, 2021)**. Owing to this “unique” response, DT plants have attracted attention for their potential genetic value in breeding drought-resistant crops **(Costa *et al.*, 2016; Hilhorst *et al.*, 2018)**. Nevertheless, they are often assumed to be inherently resistant to environmental change and consequently overlooked in conservation strategies, a misconception that is not justified nor supported by current literature. Evidence shows that DT plants can be sensitive to alterations in environmental conditions, particularly when drought intensity or duration exceeds their tolerance capacity **(Gaff, 1981; Marks *et al.*, 2021)**.

Future droughts are projected to become more extreme, less predictable, faster-developing and longer-lasting **(Sheffield *et al.*, 2012; Trenberth *et al.*, 2014)**. Climate change is already altering global biodiversity patterns and driving shifts in species distributions **(Root *et al.*, 2003; Parmesan *et al.*, 2006)**, with projections indicating substantial habitat losses. By 2085,

under warming scenarios exceeding 1.5–2.5 °C, climate change might cause up to 90% of habitat loss for some plant species in Africa (IPCC, 2007; Busby *et al.*, 2012). Such conditions could challenge the capacity of DT plants to tolerate desiccation in new climatic settings. Identifying species most vulnerable to these changes is therefore crucial for informing conservation priorities. Many DT species are closely associated with inselbergs, rock outcrops that rise abruptly from surrounding landscapes and act as island-like ecosystems to the species that inhabit them (Porembski and Barthlott, 2000; Marks *et al.*, 2021). Some of these species are specifically endemic to inselbergs, which are particularly exposed to land-use threats such as quarrying (Porembski *et al.*, 2016). Their insular nature can reduce species' capacity to migrate to new suitable habitats, increasing their extinction risk (Porembski, 2007; de Paula *et al.*, 2020; Vanschoenwinkel *et al.*, 2024). This is particularly concerning for endemic species, which tend to be more sensitive to climatic variability than widespread taxa (Gaston, 1996; Saupe *et al.*, 2015). Protecting these species would not only prevent the loss of species at greater risk of extinction but also prevent the irreversible loss of those that occur nowhere else (e.g., genetic resources of potential ecological and agricultural importance). However, there is still no strategy for which regions and species need to be prioritized for conservation, hampering more efficient conservation efforts. The absence of region-specific information on their diversity, distribution and conservation coverage limits the effectiveness of current efforts. Due to these aspects, we believe that desiccation-tolerant plants are a good model system to discuss species neglected for conservation and the potential consequences of overlooking such conservation gaps.

Beyond climate, local edaphic factors such as soil composition and texture may also shape intraspecific variation in the ecological strategies of DT plants. Plant species are known to adopt different strategies to cope with environmental stress and disturbance (Grime, 1977; Grime, 2001) and some inselberg species display remarkable morphological variation within populations that may be linked to both climatic and edaphic heterogeneity (Burke, 2003; Porembski, 2007). Such variation could also result from stochastic processes, including dispersal limitation and historical contingencies (Hubbell, 2004; Ricklefs, 2004). While climate has received substantial attention in shaping plant responses, soil-driven processes remain underexplored despite their importance for water availability, nutrient cycling and plant development (Silvertown and Charlesworth, 2001; Hulshof and Swenson, 2010). Investigating soil-plant interactions in desiccation-tolerant species is therefore critical for understanding their adaptive capacity under global change. Desiccation-tolerant plants have

been investigated for their potential use in crop improvement under increasing drought stress (**Costa *et al.*, 2016; Farrant *et al.*, 2018**). Given that Poaceae supply a large share of global calories and occupy a vast proportion of cultivated land (**Dunster, 2017**), insights from desiccation-tolerant grasses are particularly relevant. Understanding the mechanisms governing vegetative desiccation tolerance could inform the development of crops capable of thriving in more water-limited conditions (**Bartels and Sunkar, 2005; Bohnert *et al.*, 2006**). However, this presumed robustness may not surely extend across all life stages. Seedlings are particularly sensitive to desiccation due to their underdeveloped tissues, small size, and shallow root systems (**Alpert *et al.*, 2007**) and may not retain the desiccation tolerance observed in adult plants. Thus, realizing the potential of DT species requires a realistic ecological framework that acknowledges that desiccation tolerance is context-dependent, species-specific and potentially compromised by changing drought regimes.

Many plant species rely on seed dormancy to escape unfavorable conditions and persist over time in seasonally dry environments (**Venable and Brown, 1988; Gutterman, 2002; Baskin and Baskin, 2004**). By delaying germination, seeds avoid emerging during unfavorable periods that would not support seedling survival (**Donohue *et al.*, 2010**). However, this delay comes with a potential cost; as seeds age in the soil, their germination capacity may decline, reducing their contribution to the next generation and threatening long-term population persistence (**Verma *et al.*, 2003; Soltani *et al.*, 2008; Gonzales *et al.*, 2012**). While many studies have shown that increasing seed age can reduce germination rate (**Soltani *et al.*, 2008**), seedling vigor (**Joaoabba and Lovato, 1999**) and establishment success (**Verma *et al.*, 2003**), most of this evidence comes from non-desiccation-tolerant species. Previous studies showed that in species with desiccation-tolerant seeds but desiccation-sensitive seedlings, tolerance can be lost rapidly after germination (**Alpert *et al.*, 2007**). For desiccation-tolerant vascular plants, whether seed age reduces early seedling desiccation tolerance remains unclear. If seed age can affect both germination and seedling desiccation tolerance, it would challenge assumptions about the resistance of desiccation-tolerant plants and undermine the long-term benefits of dormancy and desiccation tolerance, especially under rapidly changing environmental conditions due to climate change. **Marks *et al.* (2021)** suggest that desiccation-tolerant plants may not be immune to changes in drought intensity or timing. Therefore, understanding how seed age affects early seedling desiccation tolerance is essential for predicting desiccation-tolerant plants persistence and designing conservation.

West Africa provides an ideal context for addressing these questions, as it encompasses strong climatic and edaphic gradients, forest–savanna transitions and numerous inselberg systems that host DT plants. The region faces escalating climate risks (**Venter *et al.*, 2016; WMO, 2024**), significant land-use pressures such as quarrying that directly threaten rock-outcrop floras (**Porembski *et al.*, 2016**), and contains species-rich yet poorly studied flora with high conservation value (**Myers *et al.*, 2000**). Many DT plants in this region are narrow endemics with limited dispersal ability (**Porembski, 2007; de Paula *et al.*, 2020; Vanschoenwinkel *et al.*, 2024**), making them particularly vulnerable to climatic variability (**Gaston, 1996; Saupe *et al.*, 2015**). Despite their scientific recognition and applied relevance, desiccation-tolerant vascular plants remain neglected in conservation in West Africa. There is no comprehensive, curated list of species, their conservation coverage (e.g., IUCN assessments, protected area representation) is unclear and region-wide data on their diversity, ecological strategies and projections of their responses to climate and edaphic change are lacking. For example, their unknown conservation coverage is a problem given exposure to quarrying (**Porembski *et al.*, 2016**) and climate change (**Venter *et al.*, 2016; WMO, 2024**). We still lack region-wide, species-level projections that reconcile niche-based and spatial modeling approaches that quantify changes in range size, fragmentation and centers of diversity/endemism under contrasting climate scenarios. We do not know whether soil characteristics influence intraspecific variation in CSR strategies for desiccation-tolerant plants, nor whether seed ageing compromises early seedling DT.

To address these identified gaps, this study intends to respond to the main following research question: What are the factors shaping and controlling the geographical distribution of desiccation-tolerant vascular plants in West Africa?

Based on this question, this study seeks to address the four specific questions that have been outlined to provide a detailed framework for assessing the factors influencing the distribution of desiccation-tolerant plants in West Africa: **(i)** What desiccation-tolerant vascular plant species occur in West Africa? Where are they found? What is their conservation status? To what extent are they exposed to anthropogenic pressures and how do existing protected areas mitigate this exposure? **(ii)** Where are the current centers of diversity and endemism of desiccation-tolerant plants in West Africa and how will the projected climate change scenarios affect species' geographical ranges and diversity patterns? **(iii)** Do soil characteristics shape the intraspecific variation in desiccation-tolerant plants' ecological strategies? **(iv)** Does seed age

influence the desiccation-tolerance ability of desiccation-tolerant plants under changing environmental conditions?

Building on existing ecological theory and empirical evidence, this study tests a set of theory-driven hypotheses that reflect current assumptions about desiccation tolerance while allowing for alternative outcomes. We hypothesize that available information on the diversity, distribution and conservation status of DT plants in West Africa is fragmented and incomplete, reflecting their historical neglect in regional conservation planning and that many species are exposed to anthropogenic pressures. Given the physiological ability of DT plants to cope with water stress, we further hypothesize that their responses to climate change will not be uniform, with some species maintaining relatively stable suitable habitats while others, particularly narrow endemics associated with inselbergs, may experience range contractions and increased fragmentation. At the local scale, we hypothesize that variation in soil characteristics contributes to intraspecific differences in ecological (CSR) strategies, indicating adaptive responses to edaphic heterogeneity. Finally, we hypothesize that desiccation tolerance is maintained across all life stages, such that seed ageing does not substantially reduce early seedling desiccation tolerance, thereby supporting the expectation that DT confers continuity from seeds to seedlings.

In line with these research questions and hypotheses, the main objective of this study is to provide a better understanding of desiccation-tolerant plants and the drivers that influence their current and future geographical distribution in West Africa.

Specifically, the study aims to: **(1)**. Evaluate the diversity, geographical distribution, conservation status and exposure of desiccation-tolerant plants to anthropogenic pressures in West Africa, including the potential mitigating role of the existing protected areas. **(2)**. Assess the impact of climate change on the current geographical distribution and the diversity patterns, including species richness and endemism, of desiccation-tolerant vascular plants in West Africa. **(3)**. Investigate the role of soil characteristics in influencing the intraspecific variation in desiccation-tolerant plants' ecological strategies. **(4)**. Assess how seed age affects the desiccation-tolerance ability under climate change.

By integrating biogeographical, ecological and life-history perspectives, this study seeks to provide a more realistic ecological framework for understanding desiccation tolerance and to inform more effective conservation strategies for a group of species that has been largely overlooked despite its ecological and potential applied importance.

The thesis is structured into three main parts in addition to the introduction and the conclusion sections:

- The general introduction provides the background on desiccation-tolerant plants and the context of the study;
- Part one contains a literature review on: desiccation-tolerant plants (Chapter 1); Known factors shaping the diversity of desiccation-tolerant plants worldwide (Chapter 2), climate change (Chapter 3) and the study area (Chapter 4);
- Part two provides a detailed overview of the methodological approach per objective (Chapter 5), used in this study. It described the study system, the data sampling design, the experiments conducted, the data analysis processes and the software used.
- Part three provides the main results related to each objective (Chapters 6, 7, 8 and 9), and was discussed in Chapter 10.
- Lastly, a general conclusion, research perspectives and recommendations are given, in which we highlight the most important findings and proposed knowledge gaps that could be better explored by future studies.

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## **PART ONE: LITERATURE REVIEW**

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## Chapter 1: Generalities on desiccation-tolerant plants

### 1.1. Definition and Concept of Desiccation-tolerance

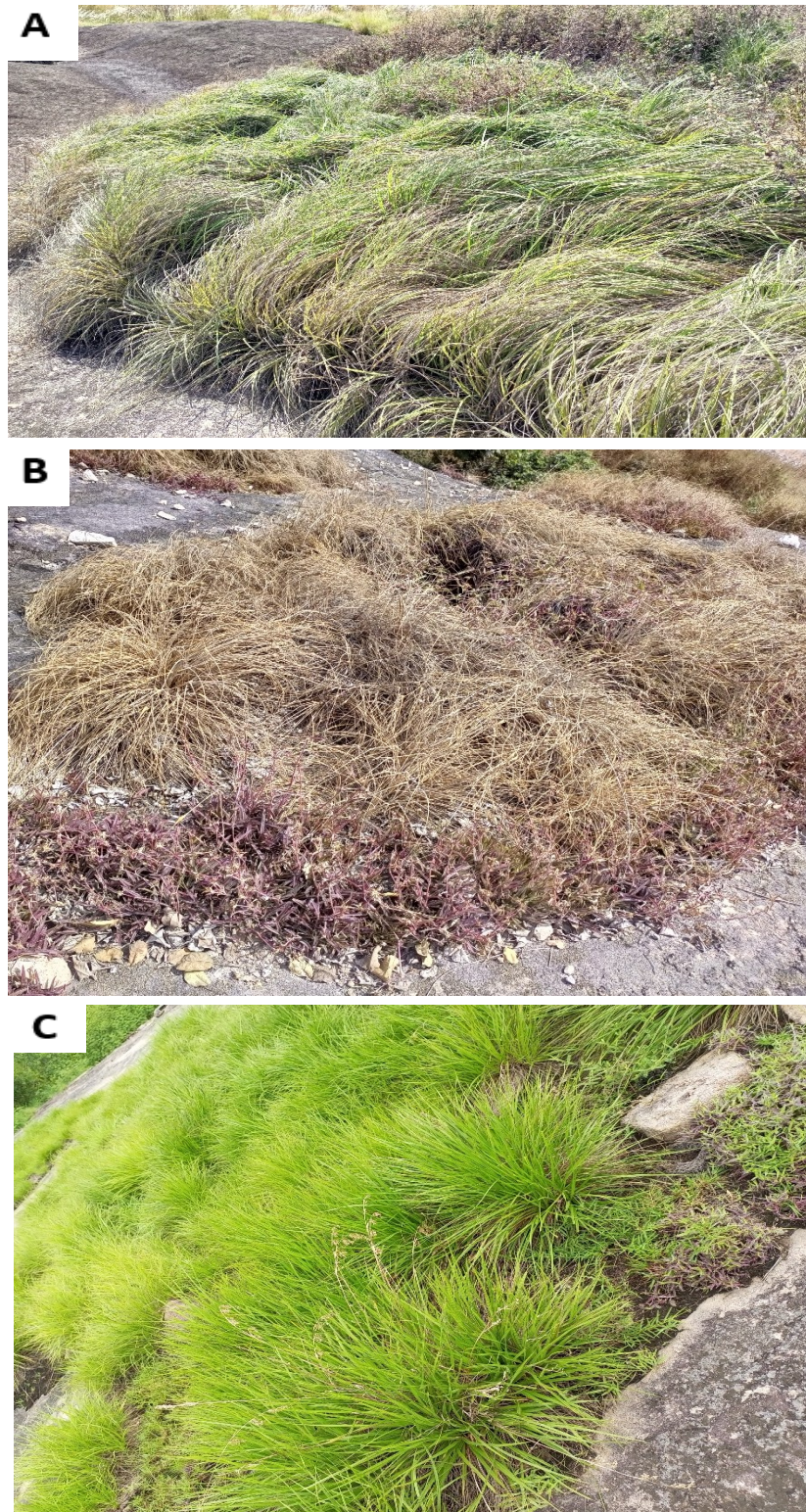
In plants, desiccation tolerance is the capacity of an organism (or its tissues and organs) to tolerate almost complete loss of protoplasmic water, reaching equilibrium with atmospheric dryness (**Bewley, 1979; Oliver *et al.*, 2000; Gaff and Oliver, 2013**). Desiccation-tolerant organisms suspend their metabolism in the air-dry state, resuming activity when moisture returns (e.g. *Afrotrilepis pilosa* (Boeck.) J. Raynal) as shown on the figure 1. According to many authors such **Bewley (1979); Vicré *et al.*, (2004); Farrant and Moore (2011)**, this phenomenon is widespread in algae, lichens and bryophytes, but rare among vascular plants, where it is mostly restricted to reproductive structures (pollen, spores, seeds). In vascular plants, desiccation tolerance of vegetative tissues is an exceptional trait that has independently evolved multiple times (**Oliver *et al.*, 2000; Marks *et al.*, 2021; Porembski, 2021**). DT vascular plants can withstand water loss below 13-20% of protoplasmic content without losing viability of photosynthetic tissues. Although rare, this adaptation is found in an estimated 1500 species worldwide, including ferns such as *Selaginella*, monocots such as Cyperaceae, Poaceae and Velloziaceae, and eudicots like Scrophulariaceae (**Porembski, 2011**).

### 1.2. Habitats and ecology of desiccation-tolerant plants

DT plants typically occur in habitats prone to rapid water loss and high solar radiation, such as rock outcrops (Figure 2), shallow soils and exposed tree canopies (**Porembski and Barthlott, 2000; Marks *et al.*, 2021**). Inselbergs (isolated rock outcrops) are considered major centers of DT plant diversity, with up to 90% of species associated with these habitats (**Marks *et al.*, 2021**). Their ecological role lies in enduring extreme fluctuations in water availability, surviving prolonged drought, and resuming growth when conditions improve. Environmental constraints shaping DT plant ecology include desiccation rate, light incidence, temperature and the intensity and frequency of drought events (**Marks *et al.*, 2021**). Future climate change, with more severe droughts (**Broennimann *et al.*, 2006; Sheffield *et al.*, 2012; Trenberth *et al.*, 2014**), may push DT plants beyond their tolerance limits. Thus, their survival strategies represent a complex ecological adaptation to some of the most hostile environments.

### 1.3. Diversity of desiccation-tolerant plants

Early estimates suggested only 60-70 vascular DT species (**Bewley, 1979**), but advances in floristic surveys and physiology have raised this number to about 1,500 (**Porembski, 2021**). DT plants occur across 11 families of ferns and allies, and 10 angiosperm families (**Marks *et al.*, 2021**).



**Figure 1.** Morphological appearance *Afrotrilepis pilosa* (Boeck.) J. Raynal during dehydration and rehydration in Côte d'Ivoire: **(A)** early desiccation stage at Mount Niangbo, November 2022 (beginning of the dry season); **(B)** fully desiccated state at Dabakala, November 2022 (dry season); **(C)** rehydrated state on Mount Niangbo, September 2025 (rainy season).





**Figure 2.** Inselberg habitat with desiccation-tolerant plants during the rainy season on Mount Niangbo, Côte d'Ivoire (September 2025), showing *Afrotrilepis pilosa*.

Two main physiological strategies underlie their ecological success: homoiochlorophylly (homoiochlorophyllous plants) which retain chlorophyll and maintain photosynthetic structures during desiccation. They can quickly resume photosynthesis after rehydration and are typically ferns, eudicots and some lycophytes; they tolerate rapid and repeated desiccation cycles. Poikilochlorophylly (referring to poikilochlorophyllous plants) dismantles the photosynthetic apparatus during dehydration and rebuilds it after rehydration. This strategy is exclusively found in monocots and confers an advantage under prolonged, high-radiation droughts (**Bewley, 1979; Oliver *et al.*, 2000; Tuba, 2008; Marks *et al.*, 2021**). However, some exceptions exist, for example, Selaginellaceae and Myrothamnaceae species, despite being homoiochlorophyllous, thrive in habitats with long droughts where poikilochlorophyllous species also occur (**Porembski, 2021**).

#### **1.4. Geographical distribution of desiccation-tolerant plants**

Desiccation-tolerant plants are found on all continents except in Antarctica (**Marks *et al.*, 2021**), and the highest diversity is found in tropical and subtropical regions, especially Africa, South America and parts of Asia where, inselbergs and rock outcrops are common. However, while it is good to know the global distribution as it is key for understanding evolutionary patterns, it should be more than necessary to know that local diversity often depends on microhabitats such as rock crevices, shallow soils or epiphytic niches.

#### **1.5. Characteristics of desiccation-tolerant plants**

DT plants exhibit a wide array of structural, physiological and molecular mechanisms to survive desiccation. Common responses include:

- **Morpho-anatomical traits:** leaf folding, trichomes, thick cuticles and small leaf area are important in minimizing the exposure to radiation and water loss (**Lebkuecher and Eickmeier, 1991; Farrant *et al.*, 2003**).
- **Physiological responses:** such as the rapid stomatal closure, the osmotic adjustment and the reduced respiration (**Eickmeier, 1979; Willigen *et al.*, 2001**).
- **Biochemical mechanisms:** accumulation of protective sugars (e.g., trehalose, sucrose), which stabilize membranes and proteins (**Kaiser *et al.*, 1985; Müller *et al.*, 1995**), production of late embryogenesis abundant (LEA) proteins, antioxidants and heat-shock proteins (**Piatkowski *et al.*, 1990; Bartels and Mattar, 2002; Juszczak and Bartels, 2017**).
- **Photosynthetic strategies:** either retaining chlorophyll (homoiochlorophyllous) or dismantling and rebuilding it (poikilochlorophyllous).

Despite the fact that those mechanisms are well studied, their ecological implications remain less explored. DT plants are sometimes described as “nearly unbeatable” against drought, able to survive

for decades in a desiccated state (**Roser, 1991; Alpert, 2000**). Yet evidence shows that their tolerance is often conditional and constrained by environmental factors (**Georgieva et al., 2008; Marks et al., 2021**).

### **1.6. Socioeconomic importance of desiccation-tolerant plants**

The ability of DT plants to withstand extreme drought has attracted scientific and biotechnological attention for agricultural and biotechnological applications, particularly for crop improvement under climate change. DT-associated genes and pathways could potentially be transferred to crops to improve drought resistance and food security under climate change scenarios (**Vicré et al., 2004; Farrant and Moore, 2011; Farrant et al., 2020**). Moreover, some DT plants (e.g., *Myrothamnus flabellifolius*) are used in traditional medicine and represent important cultural resources (**Farrant and Moore, 2011**). However, this application requires a better ecological understanding of DT responses to drought variability.

### **1.7. Conservation and threats to desiccation-tolerant plants**

Despite their ability to tolerate desiccation, DT plants remain vulnerable to environmental change. Their persistence depends not only on intrinsic physiological adaptations but also on external factors such as the frequency, duration and intensity of drought events, which are projected to increase under climate change (**Sheffield et al., 2012; Trenberth et al., 2014; Marks et al., 2021**). DT species are restricted to inselbergs and ferricretes, which face additional pressures from human activity. Major threats include habitat loss due to agricultural expansion, land-use change and direct habitat destruction through quarrying and mining (**Porembski et al., 2016**). Furthermore, the limited dispersal ability of many DT plants increases their vulnerability to habitat fragmentation.

### **1.8. Knowledge on the selected desiccation-tolerant species**

Given that grasses (Poaceae) occupy about 70% of cultivated land worldwide and play a central role in the global economy and food supply (**Dunster, 2017**), we focused on desiccation-tolerant plants also from this family. Previous successes in improving drought tolerance of rice and wheat (**Xu et al., 1996; Sivamani et al., 2000**), both Poaceae species, further justify our choice.

#### **1.8.1. *Tripogonella minima* (A.Rich.) Hochst. ex Steud**

*Tripogonella minima* is a small, slender, caespitose perennial native to Africa (Figure 3a). It typically inhabits seasonally dry tropical biomes, including rock outcrops, open grasslands and exposed slopes at elevations ranging from 90 to 1700 m. It belongs to the genus *Tripogonella* (syn. *Tripogon*), within the Poaceae family. This species is known for its ability to grow in shallow soils and xeric



microhabitats, and is considered one of the more robust desiccation-tolerant grasses of African rock outcrops (POWO, 2024).

### **Reproduction and seed dispersal**

Detailed ecological information on *Tripogonella minima* is scarce. However, available studies on the genus *Tripogonella* provide useful insights into the life-history strategies that likely influence the distribution of its constituent species. *Tripogonella* species typically exhibit an annual or short-lived perennial life cycle, enabling quick regeneration from dormant basal buds or tussock bases after rainfall in arid environments. This resurrection-like ability allows plants to revive from desiccated states, with vegetative growth resuming rapidly upon rehydration (Thoiba and Pradeep, 2020).

*Tripogonella minima*'s flowering and fruiting period spans from May to July (Thoiba and Pradeep, 2020). It has the capacity for quick flowering in response to precipitation and produces viable seeds within days of rain. Flowering in *Tripogonella* is strongly triggered by rainfall, with inflorescences emerging shortly after moisture cues to capitalize on brief wet periods. Pollination occurs primarily via anemophily (wind dispersal of pollen), typical of grasses in the Chloridoideae subfamily, though some species incorporate cleistogamous florets-self-pollinating flowers that remain closed within sheaths- to ensure reproduction under variable conditions (Thompson, 2022).

Seed (Figure 3b) production yields small, lightweight caryopses that are dispersed primarily by wind or gravity, aiding colonization of open, disturbed soils. These seeds often enter physiological dormancy to endure prolonged dry spells, preventing premature germination in unpredictable climates (Pardo *et al.*, 2020). Upon sufficient moisture, germination is rapid, with seedlings establishing quickly; in favorable wet seasons, the full life cycle from germination to seed maturity can be completed in few weeks, supporting opportunistic growth strategies (Thoiba and Pradeep, 2020).

### **Distribution in Africa**

*Tripogonella minima*, occupies a wide African range (Figure 3c), spanning from West Africa (e.g., Benin, Burkina Faso, Ghana, Mali, Mauritania, Niger, Nigeria, Senegal, Togo) through Central and East Africa (e.g., Angola, Cameroon, Chad, Ethiopia, Kenya, Sudan, Tanzania) to Southern Africa (e.g., Botswana, Eswatini, Malawi, Mozambique, Namibia, South Africa, Zambia, Zimbabwe) and Madagascar (POWO, 2024).

#### **1.8.2. *Microchloa indica* (L.f.) P.Beauv.**

*Microchloa indica* is a loosely caespitose annual or short-lived perennial, occurring in open grasslands, mopane woodlands and habitats such as roadsides and termitaria, from 610 to 2350 m in elevation (Figure 4a). It belongs to the genus of *Microchloa* within the Poaceae family and it is

ecologically plastic and adapted to drought-prone environments. This plant often germinates quickly to exploit transient moisture availability (POWO, 2024).

### **Reproduction and seed dispersal**

Although the genus *Microchloa* is well described morphologically, no reliable information on the flowering period, life cycle, or germination of *Microchloa indica* has been published to date. The inflorescence of *Microchloa* consists of a single terminal raceme, typically measuring 1.5-25 cm in length, supported by the culm and featuring a semi-terete rachis that bears spikelets in an inclined or pectinate arrangement (World flora online, 2024; Hyde *et al.*, 2026). Spikelets are small, 2-4 mm long, solitary, and comprise two glumes subtending one fertile floret (rarely two, with the second being staminate), disarticulating above the glumes at maturity (POWO, 2024). The glumes are subequal and 1-nerved, with the lower glume keeled and membranous, and the upper glume longer, firmer, and dorsally rounded. The fertile lemma is membranous, keeled, acute to two-lobed at the apex, and typically awnless or minutely mucronate, while the palea remains persistent (Hyde *et al.*, 2026). Fruits of *Microchloa* are small, ellipsoid caryopses, approximately 0.9-1.5 mm long, enclosed within the persistent lemma and palea (Burundi flora, 2026). Figure 4b shows a cleaned caryopsis after removal of surrounding floral bracts. Pollination is anemophilous (wind-mediated), with bisexual florets typical of the genus. To date, specific and clear reproductive traits and life cycle characteristics of *M. indica* remain unknown. To our knowledge, no species-specific information is available on seed dispersal mechanisms, germination ecology, or other life-history traits of *M. indica*, and key aspects of its reproductive biology and life cycle remain poorly documented in the published literature.

### **Distribution in Africa**

*Microchloa indica* is native to Angola (Figure 4c), Benin, Botswana, Burkina, Burundi, Cameroon, Central African Republic, Chad, DR Congo, Ethiopia, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Kenya, Malawi, Mali, Mozambique, Namibia, Niger, Nigeria, Senegal, Sierra Leone, Somalia, Sudan-South Sudan, Tanzania, Togo, Zambia, Zimbabwe (POWO, 2024).

#### **1.8.3. *Sporobolus festivus* Hochst. ex A. Rich.**

*Sporobolus festivus* is a densely caespitose perennial grass, which typically inhabits seasonally dry tropical biomes on sandy soils, escarpments, rock outcrops and shallow pans on laterite and calcrete; it also often occurs along roadsides (Figure 5a). This plant could be found at elevations from 90 to 1200 and it belongs to the genus of *Sporobolus*, within the Poaceae family. *Sporobolus festivus* is well-adapted to seasonally dry environments (POWO, 2024).

## Reproduction and seed dispersal

*Sporobolus* species exhibit hermaphroditic florets typical of the Poaceae family, with most species producing bisexual flowers, although monoecious tendencies have been reported in certain populations. Flowering generally occurs between June and October, with anthesis typically peaking from late morning to evening (Richard *et al.*, 2015). As wind-pollinated (anemophilous) grasses, *Sporobolus* relies on airborne pollen transfer; panicles are often enclosed within leaf sheaths during early development, providing protection to immature florets until maturity. Anthesis timing coincides with warm-season growth, enabling synchronization with favorable environmental conditions such as higher temperatures and lower humidity (Richard *et al.*, 2015).

Seed production in *Sporobolus* is characterized by self-compatibility, allowing autogamous reproduction through cleistogamous florets that remain closed, while chasmogamous (open) florets promote outcrossing in many species (Skokan, 1983). This mixed breeding system results in high fertility, with seed set ranging from 83% to 99% of florets.

The genus derives its common name “dropseed” from a distinctive dispersal mechanism in which mature caryopses detach easily from the rachilla and fall near the parent plant, promoting local colonization (Richard *et al.*, 2015). This primarily autochorous strategy may be supplemented by anemochory (wind dispersal) and zoochory through adhesion to animal fur or ingestion by herbivores. Vegetative reproduction is also important in perennial *Sporobolus* species, mainly through tillering, whereby basal shoots emerge from the crown to form dense clumps. In *Sporobolus festivus*, reproduction occurs predominantly through vegetative growth via short rhizomes that produce new axes within the same clump, while sexual reproduction is possible but seed (Figure 5b) germination is rare (Le Bourgeois, 1993). Germination in *Sporobolus* requires specific environmental cues, with optimal temperatures ranging from 20 to 30 °C. Alternating temperature regimes (e.g., 25/35 °C or 35/25 °C) further enhance germination, particularly under light exposure, while light promotes germination in some species, others exhibit similar germination rates under dark conditions (Khan *et al.*, 2003; Teimoori *et al.*, 2025).

## Distribution in Africa

According to POWO (2024), *S. festivus* is native to: Angola, Benin, Botswana, Burkina, Burundi, Cameroon, Central African Republic, Chad, DR Congo, Equatorial Guinea, Eritrea, Ethiopia, Gambia, Ghana, Guinea, Ivory Coast, Kenya, Madagascar, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Northern Provinces, Rwanda, Senegal, Somalia, Sudan-South Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe (Figure 5c).



#### 1.8.4. *Afrotrilepis pilosa* (Boeck.) J. Raynal

*Afrotrilepis pilosa* is a vigorous, perennial herbaceous plant that grows in dense tufts up to 80 cm or pads, often forming extensive mats on granite and gneiss rock outcrops (inselbergs), where it dominates steep slopes and rock faces with little to no soil (Figure 6a). Adapted to extreme conditions, *Afrotrilepis pilosa* is poikilohydric, able to survive drying out and rehydrate when moisture returns. It belongs to the Cyperaceae family and forms long-lived vegetation pads that persist for a long span.

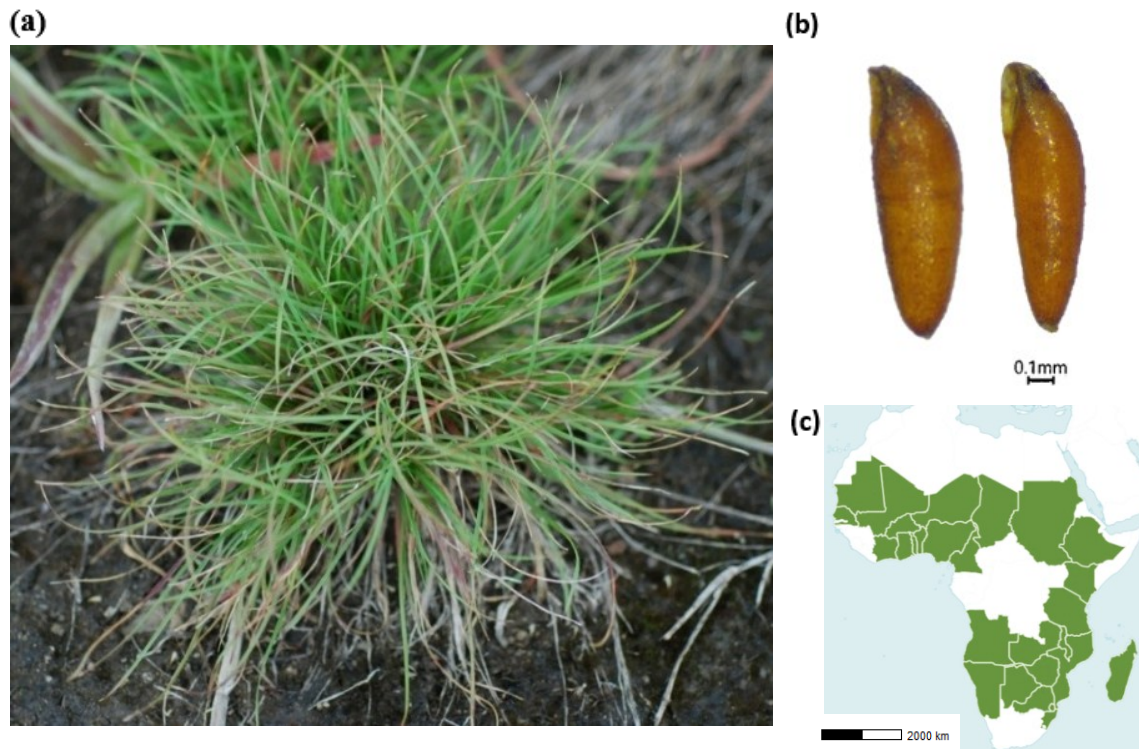
#### Reproduction and seed dispersal

The inflorescence of *Afrotrilepis pilosa* is a terminal, lax panicle measuring 15-30 cm in length and 3-10 cm in width. It is composed of tiers of whorls subtended by short leafy bracts. Each whorl bears 4-10 dense, obconical to nearly globular partial inflorescences, approximately  $5 \times 4.5$  mm in size, pale to reddish brown in colour, and consisting of several male spikelets surmounted by bisexual ones (**Brink, 2011**). Spikelets are two-flowered and may be unisexual, containing two male flowers, or bisexual, with a lower female flower and an upper male flower, rarely with two female flowers. The glumes are ovate, 3-3.5 mm long, reddish brown, and terminate in an acuminate, mucronate apex (**Burkill, 1985; Brink, 2011**). Flowers are unisexual and measure 1-2 mm in length. Female flowers possess a superior ovary topped by three stigmas, whereas male flowers bear stamens (**Brink, 2011**). The fruit is a three-angled, red-brown nutlet approximately 3.5 mm long, single-seeded, and armed with numerous white bristles about 2 mm in length (**Brink, 2011**). As members of the Cyperaceae, *Afrotrilepis* species are wind-pollinated (anemophilous), with inconspicuous flowers adapted to pollen dispersal by air currents. The persistent bristles on the nutlet enhance seed dispersal through both anemochory and epizoochory, facilitating attachment to animals as well as wind transport (**Brink, 2011**).

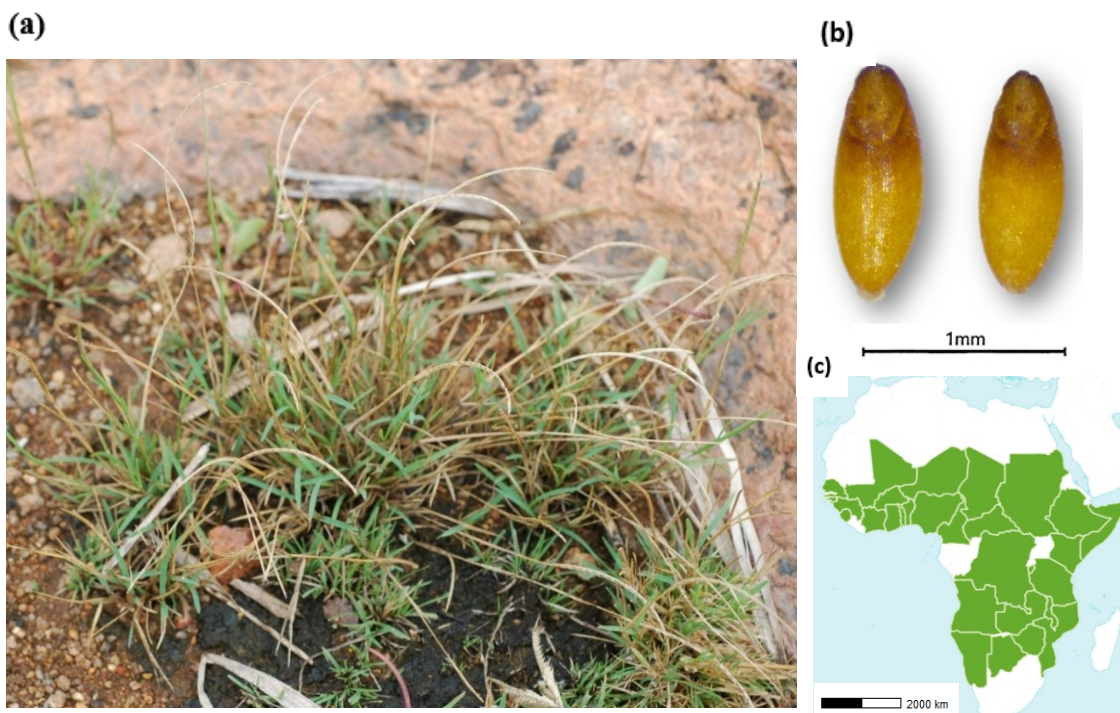
**NB:** For *Afrotrilepis pilosa*, neither mature fruits nor seeds were observed during field sampling, and no published images or detailed descriptions of the nutlet morphology could be located in the available literature or online databases. As a result, seed morphology for this species could not be documented. This absence highlights the limited reproductive information currently available for *A. pilosa* and underscores the need for further field and herbarium-based studies.

#### Distribution in Africa

*Afrotrilepis pilosa* is endemic to Western and West-Central Tropical Africa, with its overall distribution spanning from Senegal in the west to Gabon in the central region (Figure 6b). This range includes: Benin, Burkina, Cameroon, Central African Republic, Congo, Equatorial Guinea, Gabon, Ghana, Guinea, Ivory Coast, Liberia, Mali, Nigeria, Senegal, Sierra Leone, Togo (**POWO, 2024**).

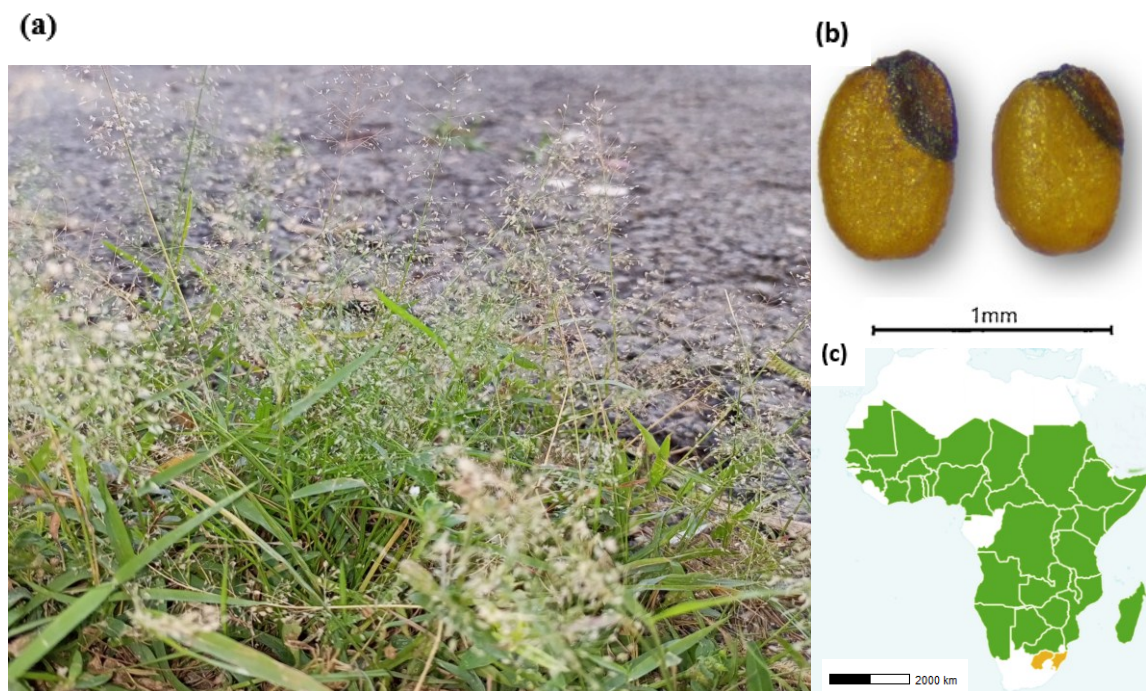


**Figure 3.** *Tripogonella minima* (A.Rich.) Hochst. ex Steud. (a) Habit of an adult plant photographed during the rainy season in Bouaké, Côte d’Ivoire (June, 2022 by S. Porembski). (b) Seeds of *T. minima*. (c) African distribution of *T. minima* based on records from Plants of the World Online (POWO, 2024).

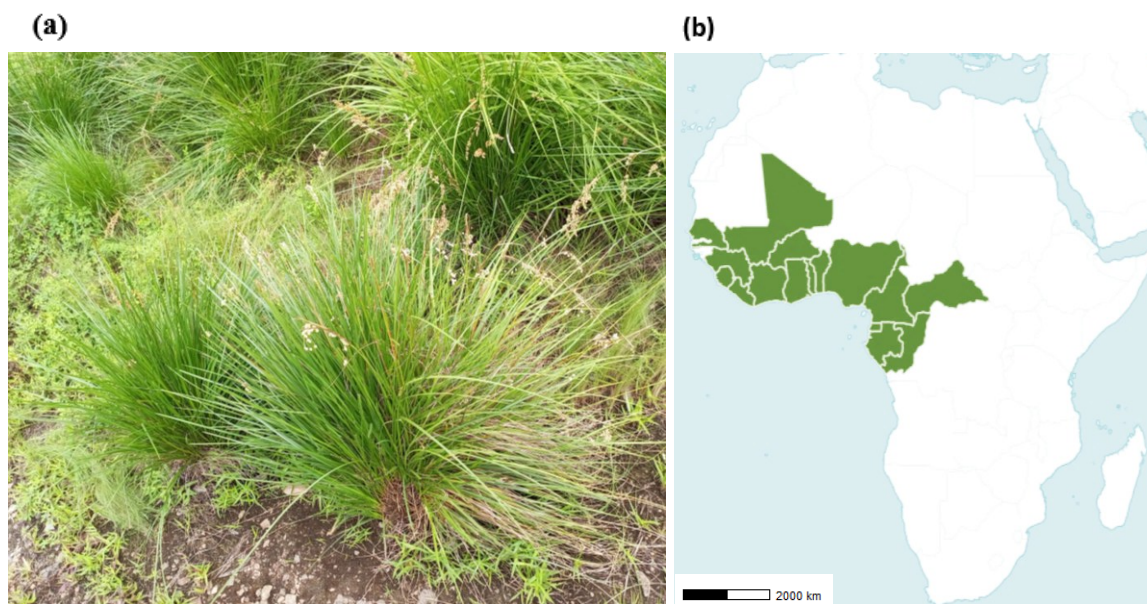


**Figure 4.** *Microchloa indica* (L.f.) P.Beauv. (a) Habit of an adult plant photographed during the rainy season in Banfora, Burkina Faso (August, 2018 by S. Porembski). (b) Seeds of *M. indica*; (c) African distribution of *M. indica* based on records from Plants of the World Online (POWO, 2024).





**Figure 5.** *Sporobolus festivus* Hochst. ex A. Rich. (a) Habit of a young plant photographed during the rainy season in Kokumbo, Côte d’Ivoire (July, 2023). (b) Seeds of *S. festivus*; (c) African distribution of *S. festivus* based on records from Plants of the World Online (POWO, 2024).



**Figure 6.** *Afrotrilepis pilosa* (Boeck.) J. Raynal (a) Habit of an adult plant photographed during the rainy season in Séguéla, Côte d’Ivoire (August, 2023). (b) African distribution of *A. pilosa* based on records from Plants of the World Online (POWO, 2024).

## 1.9. Desiccation-tolerance in seeds

Desiccation tolerance in seeds is a key adaptive trait that allows plant propagules to survive extreme dehydration and remain viable over long periods. This ability, widespread among flowering plants, is fundamental to the persistence and dispersal of terrestrial vegetation under fluctuating environmental conditions (**Bewley, 1997; Leprince *et al.*, 2017**). Desiccation-tolerance seeds, often referred to as orthodox seeds, can lose up to 95% of their water content and still germinate upon rehydration. This capacity contrasts with recalcitrant seeds, which are desiccation-sensitive and thus restricted to humid environments (**Walters, 2015**).

When considering the physiological aspect, seed desiccation-tolerance involves a complex set of protective mechanisms that stabilize cellular structures during dehydration. These include the accumulation of late embryogenesis abundant (LEA) proteins, sugars such as sucrose and raffinose family oligosaccharides, and the activation of antioxidant systems that are known to mitigate oxidative damage (**Hoekstra *et al.*, 2001; Leprince *et al.*, 2017**). Another aspect is the glassy state of the cytoplasm that results from the vitrification of soluble components; it is particularly important in maintaining the macromolecular integrity during desiccation (**Walters, 2015**).

From an evolutionary perspective, desiccation tolerance in seeds is considered ancestral and has been secondarily reactivated in a few lineages of vascular plants that evolved vegetative desiccation tolerance (**Gaff and Oliver, 2013**). For example, in arid and semi-arid ecosystems, including inselbergs, the capacity of seeds to withstand dehydration and to resume the metabolic activity after rehydration is crucial for regeneration success and population stability under irregular rainfall regimes. Therefore, understanding these mechanisms will not only provide information about the ecological strategies of DT plants but also a basis for predicting their persistence under increasing climatic variability.

This overview provides the physiological and ecological context necessary to interpret the experimental investigations on seed desiccation tolerance conducted later in this thesis.

## 1.10. Plant strategies and functional traits of the four studied species

### 1.10.1. Plant strategies

Understanding plant ecological strategies is central to explain how species respond to environmental constraints and resource availability. Plant strategies encompass the mechanisms and responses plants use to reproduce, defend themselves, survive, and compete within their environment. The term “plant strategy” has existed in the literature since at least 1965 (**Bradshaw, 1965**), and has multiple definitions. Strategies have been classified as adaptive strategies through a change in the genotype (**Bradshaw, 1965; Harper *et al.*, 1970**), reproductive strategies (**MacArthur *et al.*, 1967**), resource

allocation strategies (**Grime, 1977; 2006; Grassein et al., 2010**), ecological strategies (**Westoby, 1998**), and functional trait-based strategies (**Grassein et al., 2010; Adler et al., 2014**), to name a few. While numerous strategies exist, one underlying theme is constant: plants must make trade-offs when responding to their environment. These trade-offs and responses lay the groundwork for classifying the strategies that emerge.

The concept of plant strategies started gaining attention in the 1960s and 1970s. At this time, strategies were often associated with genotypic changes, such that plants could respond to their environment by changing their “genotypic programme” (i.e., strategy; **Bradshaw (1965); Harper et al., (1970)**). Around this same time, the r/K selection theory was introduced, which classifies plants by life history strategies, particularly reproductive strategies (**MacArthur et al., 1967; Taylor et al., 1990**). In general, plants alter their reproductive strategies (i.e., number of offspring) and their growth rate to respond to their ecological niche (**MacArthur et al., 1967; Taylor et al., 1990**). The theory is still popular in the 21st century and is frequently taught in science curricula. However, plant strategies really gained notoriety in 1977 with the introduction of Grime’s C-S-R Triangle (**Grime, 1977**), which categorizes plants according to how they respond under varying levels of stress and competition.

According to Grime (1997), plants develop strategies that demonstrate resource trade-offs between growth, reproduction, and maintenance. The association between genotypic change and strategies was also still present in Grime’s theories, as he noted that the “genotypes of the majority of plants appear to represent compromises between the conflicting selection pressures” that generally classify plants into three strategy types. The C-S-R Triangle remained the dominant plant strategy for several decades. While it does exist, additional strategies such as L-H-S strategies introduced in 1998 by Westoby (*see* **Westoby, 1998**), Grime’s C-S-R Triangle is still frequently referenced in plant ecology. This CSR framework provides a functional basis for interpreting plant adaptations across environmental gradients (**Díaz et al., 2004; Pierce et al., 2013**).

Grime identified two-factor gradients, broadly categorized as disturbance and stress, which limit plant biomass (*see* **Grime’s CSR theory 1997; 2001**). Stresses include factors such as the availability of water, nutrients, and light, along with growth-inhibiting influences like temperature and toxins. Conversely, disturbance encompasses herbivory, pathogens, anthropogenic interaction, fire, wind, etc. Emerging from high and low combinations of stress and disturbance are three life strategies commonly used to categorize plants based on environment: (1) C-competitors, (2) S-stress tolerators, and (3) R-ruderals. There is no viable strategy for plants in high-stress and high-disturbance environments, therefore categorization for this habitat type is absent (Figure 7).

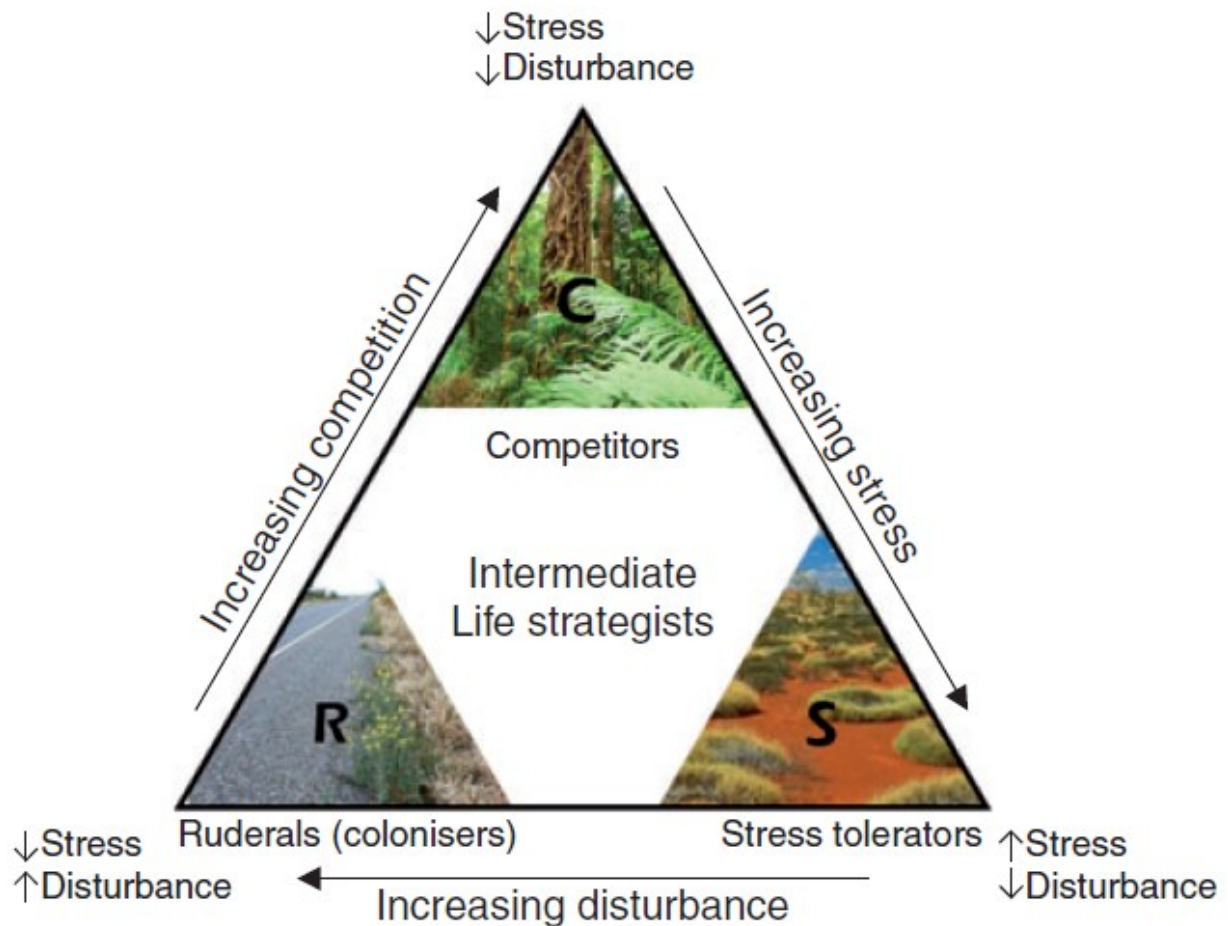
Each life strategy varies in trade-offs of resource allocation to seed production, leaf morphology, leaf longevity, relative growth rate and other factors, which can be summarized as allocation to (1) growth, (2) reproduction, and (3) maintenance. Competitors are primarily composed of species with high relative growth rate, short leaf-life, relatively low seed production, and high allocation to leaf construction. They persist in high nutrient, low disturbance environments, and “rapidly monopolize resource capture by the spatially-dynamic foraging of roots and shoots.” (Grime, 2006).

Stress-tolerators, found in high-stress, low-disturbance habitats, allocate resources to maintenance and defenses, such as anti-herbivory. Species are often evergreen with small, long-lived leaves or needles, slow resource turnover, and low plasticity and relative growth rate. Due to high stress conditions, vegetative growth and reproduction are reduced.

Ruderals, inhabiting low-stress, high disturbance regimes, allocate resources mainly to seed reproduction and are often annuals or short-lived perennials. Common characteristics of ruderal species include high relative growth rate, short-lived leaves, and short-statured plants with minimal lateral expansion.

#### **1.10.2. Functional traits and their ecological significance**

Functional traits such as specific leaf area (SLA), leaf dry matter content (LDMC) and leaf area (LA) are key plant functional traits that indicate plant ecological strategies (Grime *et al.*, 1997; Pérez-Harguindeguy *et al.*, 2013). They capture essential trade-offs between resource acquisition and conservation, growth and survival, and reproduction and dispersal (Díaz *et al.*, 2004). Measuring these traits allows the quantification of ecological strategies and links species’ functional attributes to environmental drivers such as soil depth, slope and habitat productivity (Pierce *et al.*, 2013; Negreiros *et al.*, 2014).



**Figure 7.** Diagrammatic representation of the CSR theory: Competitive, stress-tolerant, and ruderal life strategies (and their associated functional traits) form a three-way resource trade-off triangle. The selective advantage of each life strategy-and consequently the amount of resources allocated to it-are governed by levels of environmental stress and disturbance.

Where: Stress = external constraints limiting the rates of resource acquisition, growth or reproduction; Disturbance = an event causing the partial or complete destruction of cellular material. Images depict plant communities that represent typical examples of C, S or R dominated communities. (Source: Ashley Francks, 2018)

## Chapter 2: Knowledge on the factors shaping the diversity and distribution of desiccation-tolerant vascular plants

Species distributions arise from differential performance across environmental gradients and resource availability (**Chase and Leibold, 2003**). Trait-based ecology has long sought to explain these patterns by linking species traits to environmental drivers (**Funk *et al.*, 2017**). However, reliance on single traits can oversimplify species-environment relationships, as interactions among traits and trade-offs may generate alternative functional strategies with similar fitness under comparable conditions (**Shipley *et al.*, 2016; Pistón *et al.*, 2019**). Consequently, individual traits do not necessarily capture the selective forces that govern species distributions, and inferences must be drawn with caution.

DT vascular plants are commonly regarded as convergent specialists of water-deficit environments (**Gaff, 1977; Alpert, 2000; Marks *et al.*, 2021**). This view is supported by their frequent occurrence in drought-prone habitats such as rock outcrops and shallow-soil systems across multiple phylogenetic lineages. Accordingly, DT plants are often assumed to occupy the extreme end of the stress-tolerance spectrum (Figure 8), exhibiting conservative resource-use strategies that prioritize survival over growth (**Grime, 1977; Alpert and Oliver, 2002; Volaire, 2018**). This pattern implies a universal growth-survival trade-off, whereby DT plants are competitively inferior in productive environments and restricted to habitats characterized by frequent water limitation.

Despite its wide acceptance, this framework remains largely untested and may oversimplify DT plant ecology. DT plants exhibit substantial morpho-anatomical, physiological, and genetic variability in their responses to water availability (**Meirelles *et al.*, 1997; Oliver *et al.*, 2000; de Paula *et al.*, 2017; Marks *et al.*, 2021**). Species differ markedly in desiccation strategies, drought regimes, and habitat affinities, suggesting that convergent desiccation tolerance does not necessarily imply ecological equivalence or niche overlap. Empirical evidence further challenges the assumption that DT plants are uniformly poor competitors. Several studies report that some DT species achieve growth and productivity comparable to closely related desiccation-sensitive plants under favorable moisture conditions (**de Paula *et al.*, 2015; Alcântara *et al.*, 2015**), whereas others document reduced growth even when water is abundant (**Teodoro *et al.*, 2021**). These contrasting findings highlight the heterogeneity of ecological strategies among DT plants and point to unresolved questions regarding the selective processes shaping their distribution.

Much of the research on DT plants has focused on physiological mechanisms enabling survival during extreme dehydration. These studies span multiple levels of biological organization, including morpho-anatomical (**Gaff *et al.*, 1976; Tuba *et al.*, 1993**), ecophysiological (**Lebkuecher and**



Eickmeier, 1991; Georgieva *et al.*, 2020), and molecular approaches (Farrant *et al.*, 2003; Liu *et al.*, 2009; Giarola and Bartels, 2015). Recurrent mechanisms include leaf folding to reduce water loss, accumulation of protective sugars, and the production of late embryogenesis abundant (LEA) proteins that stabilize cellular structures during dehydration (Oliver *et al.*, 2020; Marks *et al.*, 2021). While these mechanisms are well documented, their ecological implications for species distributions remain poorly understood.

This gap partly stems from the widespread perception that DT plants are capable of withstanding virtually any drought condition, including prolonged periods of complete dehydration (Roser, 1991; Alpert, 2000; Griffiths *et al.*, 2014). This perception is reinforced by their frequent association with extreme environments, particularly inselbergs and other rock outcrops, which are recognized as centers of DT plant diversity (Porembski and Barthlott, 2000). Indeed, approximately 90% of DT species are estimated to occur on rock outcrops (Marks *et al.*, 2021). As a result, DT plants have attracted considerable interest as potential sources of drought-resistance traits for crop improvement under climate change (Farrant and Moore, 2011; Griffiths *et al.*, 2014; Farrant *et al.*, 2020).

However, advancing such applications requires a clearer understanding of how DT plants respond to changes in environmental conditions driven by climate change. Contrary to the assumption of drought “invincibility,” several studies have demonstrated that desiccation tolerance is context-dependent and constrained by environmental factors (Farrant *et al.*, 2003; Georgieva *et al.*, 2008). Marks *et al.* (2021) identified desiccation rate, light availability, temperature, and the frequency, intensity, and duration of drought events as key factors shaping DT plant diversity and distribution (Figure 9).

Importantly, the relative importance of these factors varies among species, underlining the multidimensional nature of desiccation tolerance and its ecological expression. Ecological differentiation among DT plants is often linked to contrasting desiccation strategies. Homoiochlorophyllous species retain chlorophyll during dehydration, whereas poikilochlorophyllous species dismantle and later resynthesize the photosynthetic apparatus (Oliver *et al.*, 2000; Tuba, 2008; Marks *et al.*, 2021). These strategies are generally associated with different environmental affinities: homoiochlorophyllous species are thought to tolerate rapid and repeated desiccation, while poikilochlorophyllous species are associated with prolonged and intense droughts under high solar radiation (Meirelles *et al.*, 1997; Alpert, 2000).

However, notable exceptions occur. Homoiochlorophyllous species within Selaginellaceae and Myrothamnaceae inhabit environments exposed to extended droughts where poikilochlorophyllous species also occur (Porembski, 2021). Such cases indicate that physiological strategy alone cannot fully explain DT plant distribution patterns. Taken together, existing studies reveal substantial

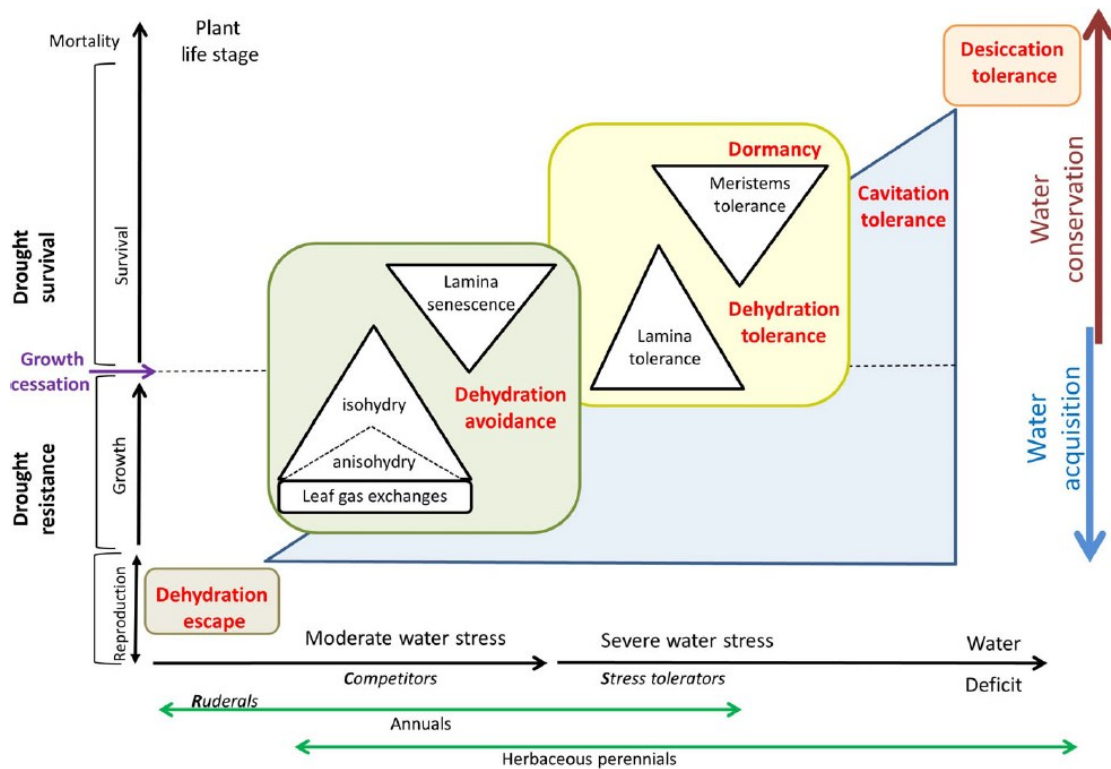
knowledge gaps regarding the ecological drivers of DT plant diversity and distribution, particularly under climate change. While DT plants predominantly occupy drought-prone habitats such as rock outcrops and forest canopies, projected increases in drought frequency, intensity, and duration may push environmental conditions beyond their physiological tolerances (**Sheffield *et al.*, 2012; Trenberth *et al.*, 2014**). This highlights the need for integrative studies that explicitly link environmental gradients to the distributions of DT plants.

Existing studies have substantially advanced understanding of desiccation tolerance at the physiological and molecular levels and, in some cases, have explored environmental drivers of DT plant distributions at local or species-specific scales. However, this body of work remains geographically uneven.

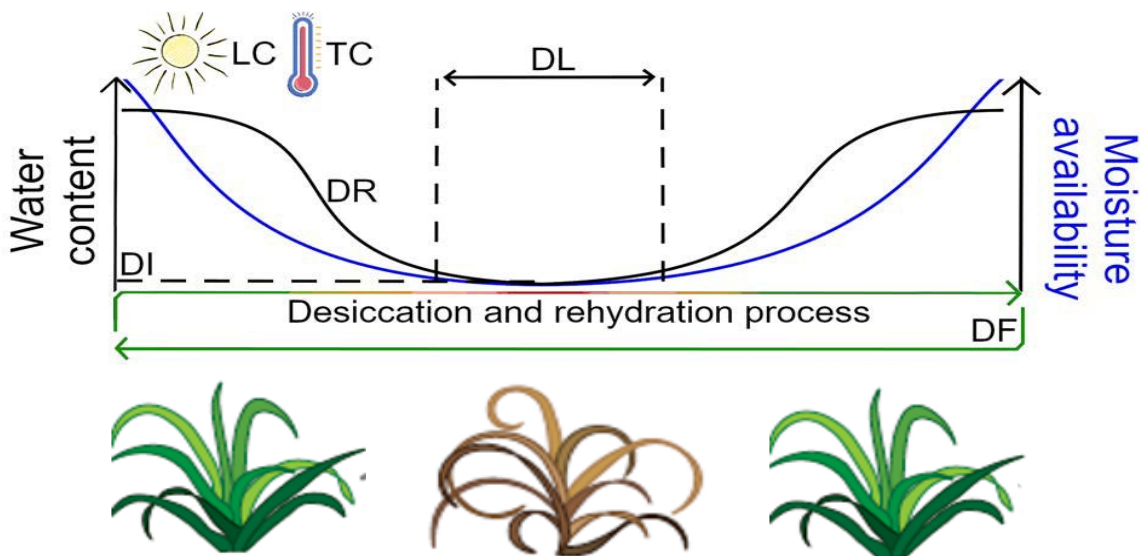
In West Africa in particular, region-scale assessments of the diversity, geographical distribution, and environmental determinants of desiccation-tolerant vascular plants are largely absent. Available studies in the region are typically taxonomically restricted, site-specific, or focused on physiological responses of individual species, limiting their capacity to inform broader biogeographical patterns.

Moreover, the degree of desiccation tolerance varies among species, and the composition of DT plant assemblages in West Africa remains poorly documented. Given that few DT species are shared among continents, it cannot be assumed that the environmental, evolutionary, or life-history drivers identified elsewhere apply directly to DT plants in this region. As a result, current knowledge is insufficient to evaluate conservation status, exposure to anthropogenic pressures, or potential climate change impacts on DT plants at a regional scale in West Africa, and the effectiveness of existing protected areas if they do exist, for conserving this functional group remains largely unknown.

This lack of regional-scale information represents a critical gap in the literature, particularly given the pronounced climatic gradients and environmental heterogeneity of West Africa, and constrains the ability, for example, to place DT plant ecology, conservation, and climate vulnerability in a broader biogeographical context.



**Figure 8:** Schematic representation of the six plant adaptive strategies to drought (dehydration escape, dehydration avoidance, dehydration tolerance, dormancy, cavitation tolerance, desiccation tolerance) for the two major responses (‘drought resistance’ with maintenance of aerial growth and ‘drought survival’ after growth cessation) along axes of increasing water deficit-water stress. Scales are time-dependent. The shapes of the symbols represent the relative contribution of the physiological adaptations and strategies to plant responses as drought intensifies (Volaire, 2018)



**Figure 9:** The desiccation-tolerant vascular plants’ response (black line) to moisture availability (blue line) along time in which desiccation and rehydration processes occur. DR - desiccation rate; LC - light incidence; TC - temperature conditions; DF - drought frequency; DI - drought intensity (dashed line); DL - drought length. Marks *et al.* (2021).

## Chapter 3: Climate change

### 3.1. Overview on climate change

Climate refers to the average pattern of weather, or more specifically, a statistical description based on the mean and variation of relevant parameters over periods ranging from a few months to several thousand years (**Faustin *et al.*, 2020**). The World Meteorological Organization (WMO) defines the reference period as 30 years (**WMO, 2017**), and the primary climate variables include temperature, precipitation and wind (**IPCC, 2013b**). Global and regional assessments by the Intergovernmental Panel on Climate Change (IPCC) confirm that Earth's climate is changing.

According to the United Nations Framework Convention on Climate Change (UNFCCC), these changes are caused directly or indirectly by human activities that modify the atmospheric composition, in addition to natural climate variability (**IPCC, 2013b**). It is currently accepted with 95% confidence that, since the late 20th century, human activities are the primary cause of observed warming (**IPCC, 2013a; Alex *et al.*, 2017**). The UNFCCC distinguishes between climate change attributable to human activities and natural climate variability (**IPCC, 2013b**). These changes will affect regions and communities differently (**Shukla *et al.*, 2022**). Globally, projected mean surface temperature increases range between +1 °C (low-emission SSP1-2.6) and +3.7 °C (high-emission SSP5-8.5) for 2081–2100 (**IPCC, 2021**).

Africa is considered one of the most vulnerable continents due to high exposure and low adaptive capacity (**Alex *et al.*, 2017**). Projections indicate that warming in Africa will exceed the global average during the 21st century (**Sanderson *et al.*, 2011; James and Washington, 2013**). Between 1880 and 2012, the global mean surface temperature increased by 0.85 °C (**Stocker *et al.*, 2013**), while between the start of the industrial era, 1850 and 1986, the increase was 0.6–0.7 °C (**IPCC, 2013a**). Precipitation projections remain more uncertain than those for temperature (**Rowell, 2012**) due to strong spatial and seasonal variability, as well as the influence of phenomena such as El Niño (**Kergomard, 2012**).

In West Africa, **Diffenbaugh and Giorgi (2012)** identified the Sahel and West African tropical zone as climate-change hotspots under RCP 4.5 and RCP 8.5 scenarios. **Mora *et al.* (2013)** predict that unprecedented climates may occur as early as the late 2030s. Many CMIP5 models indicate a wetter rainy season with a slight delay at the end of the 21st century (**Basiutti, 2013**).

## 3.2. Concepts related to climate change

### 3.2.1. Climate scenarios

A climate scenario is a plausible and often simplified representation of future climate, based on a coherent set of climatological relationships. It is mainly used to evaluate potential impacts of anthropogenic climate change using climate models.

### 3.2.2. Emission scenarios and socioeconomic pathways (SSPs)

Emission scenarios describe possible future trajectories of greenhouse gas (GHG) and aerosol emissions under different socioeconomic, technological and demographic contexts. The IPCC has successively developed:

- **IS92** in 1992 (As the first generation);
- **SRES** in 2000 (Special Report on Emissions Scenarios), as the second generation;
- **RCPs** (Representative Concentration Pathways), used in AR5, were developed in 2013.

RCPs were formerly used to describe trajectories of radiative forcing ( $\text{W m}^{-2}$ ) up to 2100 and provided the foundation for CMIP5 climate projections:

- **RCP 2.6**: radiative forcing peaks at  $\sim 3 \text{ W m}^{-2}$  before 2100, then declines.
- **RCP 8.5**: high forcing pathway exceeding  $8.5 \text{ W m}^{-2}$  by 2100.

Since the Sixth Assessment Report in 2016 (AR6), RCPs have been replaced by Shared Socioeconomic Pathways (SSPs), which integrate both radiative forcing trajectories and plausible socioeconomic development. In this study, the two SSP scenarios used are:

- **SSP1-2.6**: which is a sustainable, low-emission pathway
- **SSP5-8.5**: which is a high-emission, fossil-fuel-intensive pathway, these correspond conceptually to RCP 2.6 and RCP 8.5 but are based on updated socioeconomic assumptions in CMIP6.

### 3.2.3. Climate projections

Climate projections simulate the response of the climate system to a given scenario of GHG or aerosol concentrations. They rely on global climate models (CMIP) to estimate future variations in temperature, precipitation and climate extremes (**Moss *et al.*, 2008; IPCC, 2018**).

Projected climatic conditions in West Africa showed significant temperature increases and shifts in rainfall regimes throughout the 21st century. Based on CMIP6 projections under the SSP1 (low-emission) and SSP5 (high-emission) scenarios (Table I), the region is expected to experience more frequent droughts, higher evapotranspiration rates and a general decline in soil moisture (**IPCC, 2021**).

**Table I.** Projected climatic trends in West Africa under two emission scenarios (SSP1 and SSP5) and their main implications for ecosystems (2081-2100 relative to 1981-2010).

| Climatic variables                        | SSP1                                       | SSP5                                | Main trends/implications                                                                  |
|-------------------------------------------|--------------------------------------------|-------------------------------------|-------------------------------------------------------------------------------------------|
| <b>Mean annual temperature</b>            | +1.5 to +2.0 °C                            | +3.5 to +5.0 °C                     | High warming across the Sahelian and Sudanian zones. ; increased frequency of heatwaves.  |
| <b>Maximum temperature</b>                | +1.8 to +2.5 °C                            | +4.0 to +5.5 °C                     | Higher risk of heat stress for vegetation and livestock with a short growing season.      |
| <b>Minimum temperature</b>                | +1.3 to +1.8 °C                            | +3.0 to +4.5 °C                     | Reduced diurnal temperature range, with effects on plant phenology and respiration.       |
| <b>Annual precipitation</b>               | ±0 % to +5 %<br>(high spatial variability) | –10 % to +10 %<br>(model-dependent) | High uncertainty, with shorter but more intense rainy seasons.                            |
| <b>Number of consecutive dry days</b>     | +2 to +5 days/year                         | +10 to +20 days/year                | Longer and more frequent droughts.                                                        |
| <b>Potential evapotranspiration (PET)</b> | +3 % to +6 %                               | +8 % to +15 %                       | Intensification of water stress.                                                          |
| <b>Soil Moisture Index</b>                | Slight decline<br>(–0.2 to –0.5)           | Marked decline<br>(–1.0 to –1.5)    | Soil moisture decreased, reducing the productivity with a higher risk of desertification. |

Source: IPCC, 2021 (*Intergovernmental Panel on Climate Change, Sixth Assessment Report*).

### 3.3. Impacts of climate change on biodiversity in West Africa and implications for desiccation-tolerant plants

West Africa is one of the regions most vulnerable to climate change due to high exposure and limited adaptive capacity (Sanderson *et al.*, 2011; Alex *et al.*, 2017). Sahelian and Guinean ecosystems already show signs of increased water stress, habitat fragmentation and shifts in species distribution (Diffenbaugh and Giorgi, 2012; Mora *et al.*, 2013).

- **Rainfall variability and increased drought:** Climate projections indicate an increase in both the frequency and intensity of droughts in several areas, particularly northern Côte d'Ivoire, Mali and Burkina Faso, along with high interannual rainfall variability (Rowell, 2012; IPCC, 2021). Drought indices such as the Standardized Precipitation Index (SPI) and the Standardized Precipitation Evapotranspiration Index (SPEI) corroborate trends toward longer, more frequent, and more severe periods of water deficit. Such changes are expected to affect plant physiological performance, survival, and spatial distributions, especially in ecosystems already operating near their climatic thresholds.
- **Effect on vegetation:** changes related to precipitation and temperature regimes are projected to reduce primary productivity, disrupt regeneration processes, and alter floristic composition (IPCC, 2021), with species having restricted ranges or specialized habitat requirements being particularly vulnerable to rapid. These effects are likely to be pronounced in drought-prone habitats such as rock outcrops and shallow-soil systems, which host a large proportion of DT vascular plants.

Despite their ability to survive extreme dehydration, DT plants are not necessarily insulated from the ecological consequences of climate change. To the best of our knowledge, no studies have assessed, at a regional scale, how projected climate change scenarios may affect the geographical distribution, diversity patterns, or conservation status of DT plants in West Africa. This represents a critical knowledge gap, as changes in drought frequency, intensity, duration, and timing may interact with species-specific desiccation strategies, potentially exceeding physiological tolerances or altering habitat suitability. Consequently, assumptions that DT plants will universally benefit from or remain unaffected by increasing drought are not supported by empirical evidence. The absence of region-scale assessments linking climate change to DT plant distributions currently limits our capacity to evaluate their vulnerability, anticipate shifts in centers of diversity and endemism, or assess the relevance of existing protected areas under future climates. Addressing this gap is essential for understanding how climate change may reshape DT plant biogeography in West Africa and for informing conservation strategies for this unique functional group.

## Chapter 4: Generalities on the study area

### 4.1. Geographical location of West Africa

West Africa extends between latitudes 4°N and 28°N, and longitudes 16°W and 15°E, covering approximately 6.1 million km<sup>2</sup> (Figure 10). The region is bounded by the Sahara Desert to the north, the Atlantic Ocean to the west and south, and merges gradually into Central Africa to the east. Politically, West Africa comprises 16 countries: Benin, Burkina Faso, Cape Verde, Côte d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone and Togo. However, for ecological purposes, West Africa is often defined more broadly, extending from Senegal to Equatorial Guinea and including parts of Cameroon, Chad and Equatorial Guinea, encompassing humid and transitional vegetation zones, as described by the *Encyclopædia Britannica* (Fage and McCaskie, 2025). Although these latter countries are politically classified under Central Africa, they share strong ecological and floristic continuity with the West African forest zone (White, 1983; Fage and McCaskie, 2025). This biogeographic definition captures the region's major climatic and ecological gradients, ranging from the hyper-arid Sahelian margins in the north to the humid Guinean forests in the south. The study area is characterized by marked variation in physical features, climate, and vegetation, reflecting the influence of both latitudinal rainfall gradients and physiographic factors (more detailed descriptions of West Africa's geography and environmental characteristics can be found in White and Gleave (1971), Thomas (1973), Hance (1975), and Grove (1978)).

### 4.2. Climate of West Africa

According to Nicholson (2013), the climate of West Africa is primarily influenced by the West African Monsoon (WAM), which is controlled by the seasonal migration of the Intertropical Convergence Zone (ITCZ). Rainfall varies markedly along a latitudinal gradient, from 200-250 mm annually in the arid Sahelian zone to 2,000-3,000 mm in the humid forest regions along the Guinean coast (Biasutti, 2019). From 1991 to 2020 the rainfall mean in West Africa was about 1226mm and the temperature about 25° C (Figure 11); in the Sahel the mean of the rainfall is 388mm with 27.8° C as mean temperature (Appendix 1), In the Gulf region (humid zone) the rainfall is 1677mm and 26.6° C as mean temperature (Appendix 1). This rainfall distribution shapes four major vegetation zones: the Guineo-Congolian Zone (regional center of endemism), the Guineo-Congolian/Sudanian transition zone, the Sudanian Zone (regional center of endemism), and the Sahelian Zone (transitional zone). The climate is characterized by two main seasons, wet and dry, resulting from the alternation of two migrating air masses. The first is the tropical continental air mass from the north, associated with hot, dry Harmattan winds blowing from the Sahara between November and February. The



second is the moist tropical maritime air mass, which brings southwesterly winds and rainfall during the wet season, reaching its maximum northern extent (18°- 21°N) in July. The boundary between these two air masses, the ITCZ, shifts seasonally with the apparent movement of the sun, controlling the onset and retreat of rainfall across the region **(FAO, 1985)**.

West Africa is highly sensitive to climate variability. Since the 1970s, recurrent droughts, especially in the Sahel, have caused major ecological and socio-economic impacts **(Hulme, 2001; Nicholson, 2005)**. Climate projections indicate an increase in the frequency of extreme droughts and shifts in rainfall seasonality, which threaten agricultural productivity and biodiversity **(Sylla *et al.*, 2016)**, including specialized vegetation such as desiccation-tolerant plants.

#### **4.3. Soils and edaphic conditions of West Africa**

The geology of West Africa is dominated by ancient crystalline rocks of the Basement Complex, which form resistant uplands such as the Guinean Highlands, the Adamawa Plateau and the Atakora Range. Equally resistant older sedimentary rocks, mainly sandstones, give rise to prominent uplands and escarpments, including the Fouta Djallon Highlands in Guinea, the Banfora in Burkina Faso, the Hombori Mountains in Mali and the Gamkaza and Manpong uplands in Ghana. In contrast, younger sedimentary formations extend across large parts of southern Nigeria, Togo, Benin and Senegal-gambia **(Thomas, 1973; Grove, 1978)**. Soils across the region are predominantly deeply weathered, nutrient-poor Ferralsols and Acrisols, typically characterized by low organic matter content **(White, 1983)**. In drier zones, particularly in the Sahel and on rocky outcrops, Arenosols and shallow Leptosols dominate. These habitats are often edaphically extreme, creating microenvironments that support stress-adapted plant communities, including species with high levels of endemism **(Porembski and Barthlott, 2000; Burke, 2003)**. Soil fertility, depth and texture strongly influence vegetation structure and community composition, while rocky outcrops and inselbergs provide key refugia for desiccation-tolerant plants **(Porembski, 2007)**.

#### **4.4. Hydrology of West Africa**

West Africa is characterized by a broad undulating plateau lying mostly below 500 m above sea level, bordered by coastal plains that are widest in Senegal, southern Côte d'Ivoire, the Niger Delta and the lower valleys of the Niger and Volta rivers **(White, 1983; FAO, 1985)**. Isolated highlands rise above the plateau, including the Fouta Djallon (1,537 m), Guinea Highlands (1,656 m), Sierra Leone, like the Loma mountains (1,948 m), Jos Plateau (1,690 m), Adamawa Highlands (2,042 m) and the Aïr Massif in Niger (1,850 m). These upland areas serve as important watersheds, influencing rainfall distribution and river systems, while also hosting distinct montane ecosystems. The region's drainage

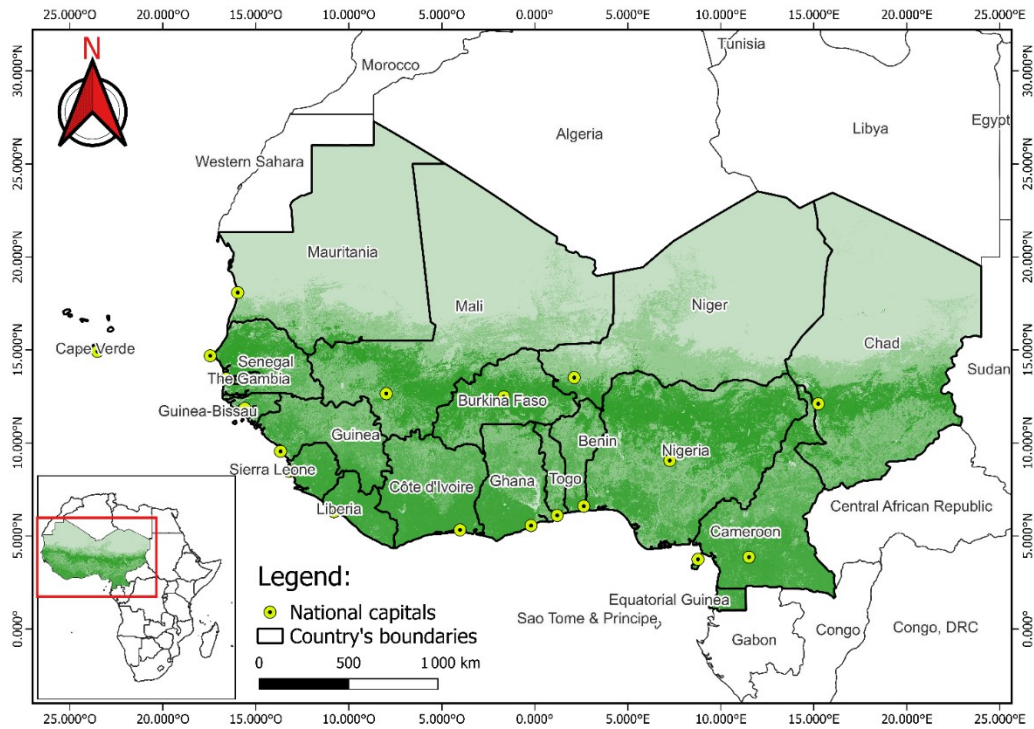
is dominated by five major river systems. The Niger River, West Africa's largest, originates in Guinea and flows northeast into Mali before turning southeast through Nigeria to the Gulf of Guinea, covering about 4,160 km (**Grove, 1978**). Other major systems include the Senegal and Volta rivers, numerous short rivers draining from the Fouta Djallon into the Atlantic, and rivers flowing into inland basins such as Lake Chad (**Hughes and Hughes, 1992**). Seasonal variability in rainfall strongly influences river discharge, leading to pronounced differences between wet- and dry-season flows. Several dams, such as Akosombo on the Volta and Kainji on the Niger, provide hydroelectric power and irrigation but also alter natural flood regimes and associated ecosystems. Together, relief and hydrology shape the region's ecological zonation, agricultural potential, and the distribution of specialized habitats such as gallery forests and floodplain wetlands.

#### **4.5. Vegetation of West Africa**

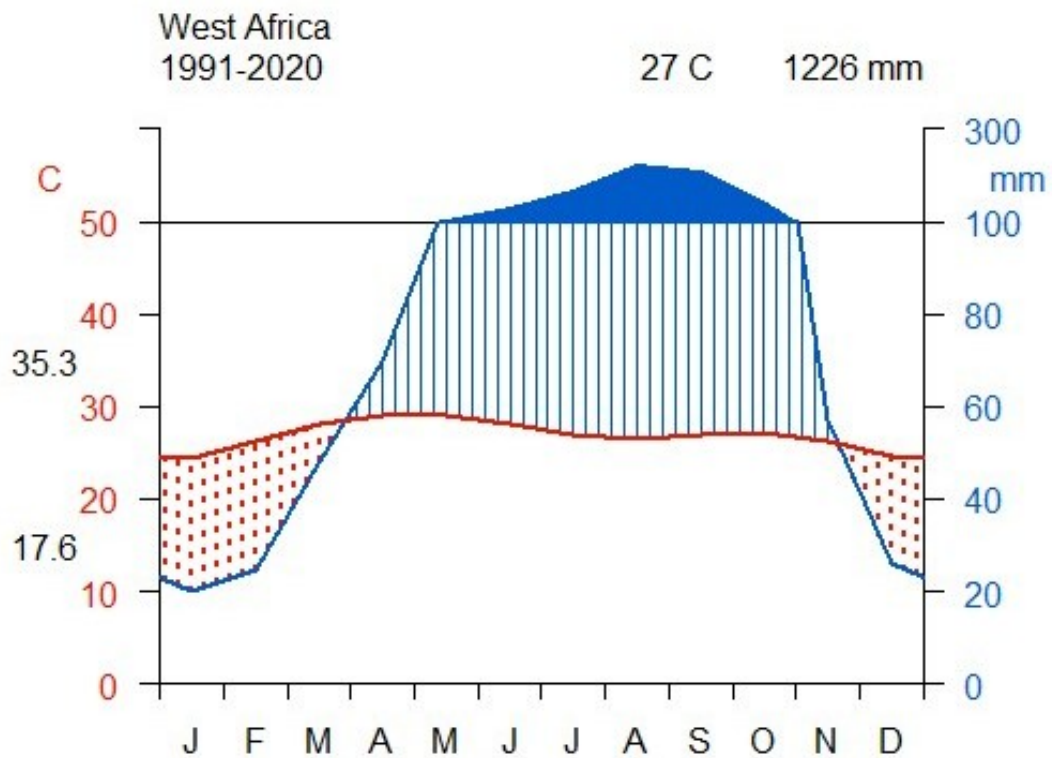
The vegetation of West Africa reflects the strong north–south climatic gradient, ranging from arid to humid environments. The northern Sahelian zone is dominated by grasslands and drought-tolerant shrubs, while the Sudanian zone supports savannas and open woodlands. Further south, the Guinean zone transitions into dry forests and moist evergreen forests, forming some of the most species-rich ecosystems in Africa (**White, 1983**). One of the most important ecosystems in this region is the Guinean Coastal Forest, which served as a refuge for many species during historical climate fluctuations in the Pleistocene. Today, it remains one of Africa's eight biodiversity hotspots, characterized by high species endemism. However, only 15% of its original forest cover remains (**Myers *et al.*, 2000; Sinsin *et al.*, 2010**), motivating conservation efforts, in which 90% of national protected areas are forests (**IUCN, 2015**), though many important ecosystems remain underrepresented, unless embedded in protected areas. Among these underrepresented systems are inselbergs and ferricretes, which form ecologically unique microhabitats often isolated from the surrounding vegetation. These rocky outcrops harbor specialized plant communities, including many desiccation-tolerant “resurrection plants,” which persist under extreme edaphic and microclimatic conditions (**Porembski *et al.*, 1996; Oliver *et al.*, 2000**). Their role as biodiversity reservoirs and natural laboratories for studying plant adaptation to water stress makes them of particular importance to this study. Although climatic gradients largely structure vegetation zonation, human activities, notably agriculture, grazing, burning and logging, have substantially reshaped West Africa's landscapes. Forests have been reduced to fragments and savannas expanded, creating mosaics of derived vegetation (**Adejuwon, 1976**). These anthropogenic modifications have both eroded natural habitats and created novel environments that influence the distribution and persistence of plant species, including DT taxa.

#### **4.6. Socio-ecological context of West Africa**

West Africa is one of the most densely populated and fastest-growing regions in Africa, with its population rising from 70 million in 1950 to 446 million in 2023 (**UN DESA, 2024**). Inhabitants whose livelihoods largely depend on agriculture, livestock and forest resources (**Mortimore, 2009**). Subsistence farming and pastoralism dominate, leaving ecosystems highly vulnerable to climate variability and land-use change. Land degradation, overexploitation and recurrent drought events threaten biodiversity and ecosystem services (**IPBES, 2018**). Furthermore, weak institutional capacity and high reliance on climate-sensitive activities make local communities particularly vulnerable to climate change (**Roudier *et al.*, 2011**).



**Figure 10.** Map of the study area: West Africa



**Figure 11.** Ombrothermic curve showing average precipitation (mm) and temperature (°C) from 1991 to 2020 for West Africa (from Mauritania to Equatorial Guinea; data source: **Climate Change Knowledge Portal, 2025**). The red color = Temperature, and the blue color = Precipitation.

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## **PART TWO : METHODOLOGY**

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## Chapter 5: Methodology

### 5.1. Evaluation of the diversity, distribution, conservation status and the exposure to anthropogenic pressures of desiccation-tolerant plants in West Africa.

#### 5.1.1. Desiccation-tolerant vascular plants in West Africa

A systematic literature review was conducted to obtain a list of DT vascular plants and to evaluate their conservation concerns in West Africa. For this, the following keyword combination was applied: “desiccation tolerant” OR “resurrection” AND angiosperm\* OR pteridophyte\* OR lycophyte\* OR vascular OR plant\*” across four search engines (1) Scopus, (2) Web of Science, (3) Academia and (4) Google Scholar. The search covered the period 1950-2024.

A total of 1657 documents were initially retrieved (243 from Scopus, 567 from Web of Science, 36 from Academia, and 811 from Google Scholar). After removing 549 duplicate records, 1322 documents were excluded because they were either not peer-reviewed (e.g., grey literature) or were not considered in the scope of our study, such as publications that did not focus on plants as their main research objective (e.g., studies on geology or zoology).

Four additional key articles (**Porembski, 2000; Tindano *et al.*, 2023a; Tindano *et al.*, 2023b; Tindano *et al.*, 2024**) were added manually, as they met the criteria (*see* keywords combination of the literature review) and are relevant to DT plant research but were not found by the abovementioned keyword search. In total, 339 publications met our criteria and were retained and analyzed.

A comprehensive list of DT vascular plant species was compiled from the literature reviewed. Species geographical distribution data and conservation status within West Africa were obtained from *The Flora of West Africa* (**Hutchinson *et al.*, 1958**), *Flora of savannas and rock outcrops of Côte d’Ivoire* (**Adjanohoun, 1964**), and Plants of the World Online (**POWO, 2025**). Occurrence data were aggregated at the country level to describe and discuss species distribution patterns and estimate the diversity patterns (species richness) of DT plants in West Africa (calculating species richness by country, i.e., number of different species occurring in the same country).

The following countries were considered in our study: Benin, Burkina Faso, Côte d’Ivoire, Cameroon, Cabo Verde, Chad, the Gambia, Ghana, Guinea, Guinea-Bissau, Equatorial Guinea, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone, and Togo. This study followed the classification of Plants of the World Online (**POWO, 2025**) and grouped into the Gulf of Guinea, the islands of Bioko, Príncipe, São Tomé and Annobón.

### 5.1.2. Assessment of the exposure of DT plants to anthropogenic pressures on West African inselbergs and the role of protected areas

To further assess the vulnerability of DT plants to major anthropogenic pressures and the potential role of protected areas in mitigating them, a case study focusing on West African inselbergs was conducted, using the database developed by S. Porembski, which compiles extensive field observations conducted between 1986 and 2024. Only inselbergs from this database were considered in the analyses.

A total of 123 inselbergs, spanning from Guinea to Equatorial Guinea, were sampled (Figure 12). From this dataset, 10 DT plants were selected with distinct and overlapping distributions across West African inselbergs: *Asplenium stuhlmannii* (Aspleniaceae); *Phymathosorus scolopendria* (Polypodiaceae); *Pellaea doniana* (Pteridaceae); *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae); *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minima* and *Sporobolus festinus* (Poaceae); and *Craterostigma yaundense* (Linderniaceae). These species form a diverse set of DT plants from taxonomic and geographical perspectives.

#### - *Conservation efforts concerning the 10 selected species*

As a rough descriptor of the conservation efforts for each species, the number of inselbergs in which each species exists that are included in protected areas and other effective area-based conservation measures was counted using the World Database on Protected Areas (UNEP-WCMC, 2024). Those inselbergs in which species exist were categorized into two groups: protected and unprotected. For the species' exposure to anthropogenic drivers of biodiversity loss, land use change and climate change were considered.

Anthropogenic drivers of biodiversity loss considered in this study were (i) land-use change, specifically quarrying activities on inselbergs, and (ii) climate change, assessed through projected shifts in species distribution under future climate scenarios. These pressures were selected based on their documented impact on desiccation-tolerant plants (see Porembski *et al.*, 2016).

They were prioritized because inselberg ecosystems are particularly exposed to quarrying, while climate change represents a major large-scale driver of environmental change in West Africa.

More broadly, global assessments such as those by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services highlight habitat change and climate change among the leading drivers of biodiversity loss worldwide (Bellard *et al.*, 2022), although the relative importance of threats may vary across regions and taxa. This context supports the focus on these key pressures in the present study.

- ***Exposure to quarrying of the 10 selected species***

To estimate exposure to land-use change, the optical evidence of quarrying activities was evaluated on the 123 inselbergs where the 10 model species occur. For this, Google Earth Engine, which is a cloud-based geospatial analysis platform (**Gorelick *et al.*, 2017**), and Sentinel-2 imagery (QA60 band) were used. A 2 km radius buffer was applied around each inselberg based on geographic coordinates from the S. Porembski database. Composite images were generated for the period October and December of 2022 and 2023, applying a cloud mask cloud cover of less than 5%) to ensure data quality (Figure 13 and Figures A3-A5, Appendix 2), and the selection of the same months across consecutive years (2022 and 2023) minimizes seasonal variability.

- ***Exposure to climate change of the 10 selected species***

To estimate exposure to climate change, the departures in climatic variables for the inselbergs where the selected DT plants exist were used. For this, two approaches were used: the modelling technique MaxEnt and climate niche factorial analysis (CNFA). First, species distribution was modeled for each species using the distribution records of species available in the database Global Biodiversity Information Facility (**GBIF, 2024**; Appendix 2, Table A1). The species occurrence data were harmonized, eliminating duplicates, errors and uncertain geographic entries. The information provided by the database Plants of the World Online (**POWO, 2025**) was used as a reference for the natural occurrence of species. Also, records that, despite a lack of geographic coordinates, were retained, including the detailed location information. Here, the centroid of the municipality was employed.

To model species distribution, the modelling technique MaxEnt (**Phillips *et al.*, 2004**) and the bioclimatic variables (Appendix 2; Table A2) available in the CHELSA dataset (**Karger *et al.*, 2023**) were used at a spatial resolution of 2°30'. Bioclimatic variables Bio6, Bio9, Bio10 and Bio11, which represent temperature extremes and seasonal means, were excluded due to their high collinearity with the other variables. Removing them reduces redundancy and helps avoid overfitting in climate-based models, ensuring more robust and interpretable results.

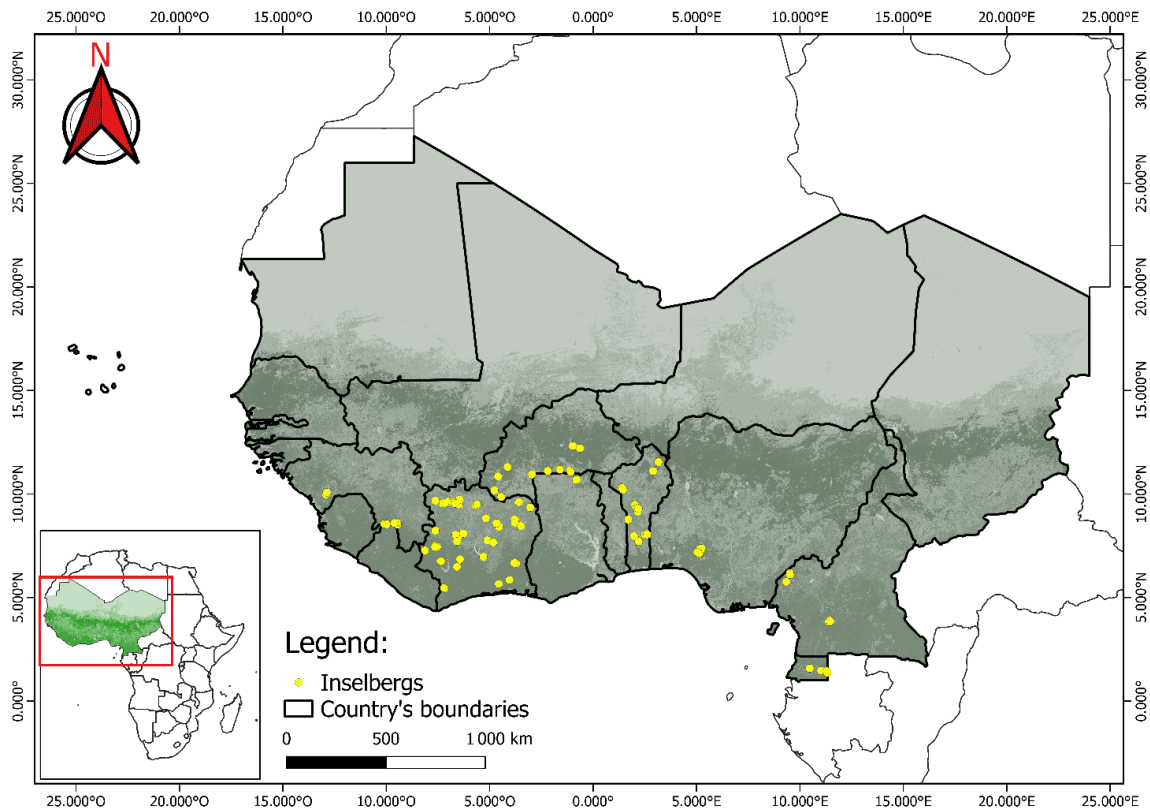
The MaxEnt technique was chosen because of its high predictability to identify suitable areas of occurrence for species from a niche-based perspective, even for taxa with only a few occurrence data (**Wisz *et al.*, 2008**). Only one observation within a 1 km radius was used, and the most important environmental variables for each modelled species with a low level of correlation were selected. These steps were considered to mitigate sampling bias effects (assuming that species populations are



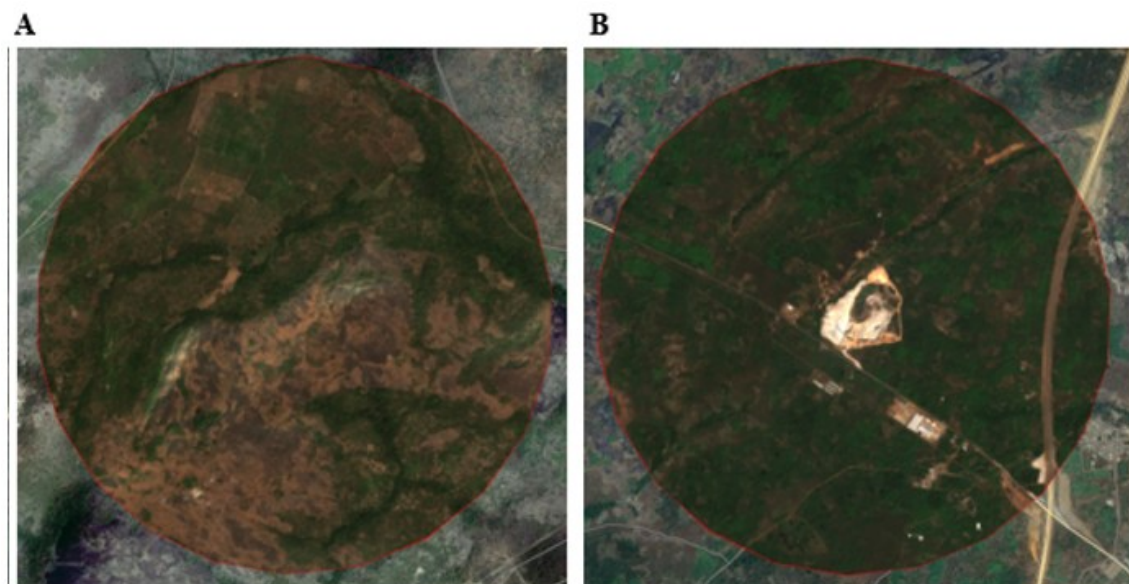
found within isolated rock outcrops and more than one sampling point can be registered for the same inselberg) and to avoid issues with multicollinearity and model overfitting.

Second, climate niche factorial analysis (**Rinnan *et al.*, 2019**) was conducted to obtain information about shifts in climatic variables within the inselbergs. Climate niche factorial analysis was conducted using the same most important bioclimatic variables that explain each species' distribution. In this analysis, the present conditions were compared to the future conditions. For the future, two Representative Concentration Pathway scenarios were used, with SSP1 being the less-severe (sustainable path with environmental boundaries and low greenhouse gas emissions) and SSP5 being the worst (very high greenhouse gas emissions, with fossil-fueled development). Also, three intervals of time-series were considered: 2011-2040, 2041-2070 and 2071-2100.

Climate niche factorial analysis was chosen for its ability to calculate departures from the prevailing climatic conditions across grid cells and provide a single exposure value for each species to climate change. This overall value of departure allows for robust comparison between species, especially when different variables were selected in order to take into consideration species individual sensitivities to environmental conditions (**Rinnan *et al.*, 2019**).



**Figure 12.** Map showing the location of the 123 inselbergs used to assess the exposure of the 10 selected desiccation-tolerant species to quarrying and climate change.



**Figure 13.** Examples of inselbergs in Côte d'Ivoire with and without quarrying, derived from Google Earth Engine imagery. **A)** Mont Niangbo (no quarrying); **B)** Inselberg in Bouaké (with quarrying).

## 5.2. Assessment of the impacts of climate change on desiccation-tolerant plant distribution and diversity

### 5.2.1. Species list and distribution models

#### ▪ Species list and occurrence data

A systematic literature review was conducted to compile a list of DT plants from West Africa. For that, four search engines were used (1) Scopus, (2) Web of Science, (3) Academia and (4) Google Scholar, and the key-words “desiccation tolerant” OR “resurrection” AND angiosperm\* OR pteridophyte\* OR lycophyte\* OR vascular OR plant\*” to retrieve every record from 1950 to 2024. A total of 1657 documents were initially retrieved (243 documents from Scopus, 567 from Web of Science, 36 from Academia, and 811 from Google Scholar), of which 549 were removed for being considered duplicate records. In the list was included every species described as a DT plant with native occurrence to West African countries according to Plants of the World Online (**POWO, 2024**). Only taxa described at the specific level were included in that list, and their nomenclature was harmonized following the Tropicos taxonomic backbone (**Tropicos, 2024**). Then, the occurrence records for each species were retrieved using the datasets with preserved specimens from the databases Global Biodiversity Information Facility (**GBIF 2024**, Appendix 3; Table A10) and Tropicos (Tropicos, 2024). Duplicated records were removed, besides data with geographic inconsistencies (e.g., country centroids or occurrences beyond species native occurrence range), with the aid of the R package “CoordinateCleaner” (**Zizka *et al.*, 2019**) and the Plants of the World Online (**POWO, 2024**). However, for records without coordinates but with the description of the collection site, the geographic entity of the location described or the centroid of the closest municipality was used with the aid of R package “ggmap” (**Kahle and Wickham, 2013**). To avoid sampling bias, multiple records for the same species were reduced within an area of 1 km radius to only one occurrence using R package “humboldt” (**Brown and Canaval, 2019**).

#### ▪ Species distribution modeling

The filtered occurrence data were used to generate species distribution hypotheses for each DT plant species to better understand their diversity patterns and identify priority conservation areas in West Africa. Two complementary modeling approaches were employed:

- A niche-based approach, in which the Maximum Entropy technique was conducted under a climate niche perspective (**MaxEnt; Phillips *et al.*, 2004**),
- and secondly, a spatial-based technique, the inverse-distance weighted (**IDW; Shepard, 1968**), by interpolating the known occurrence points for each species.

Species with fewer than five unique occurrence records were excluded from modeling. All analyses were performed at a spatial resolution of  $2^{\circ}30' \times 2^{\circ}30'$ , extending the study grid by  $5^{\circ}$  of latitude and longitude beyond the outermost species occurrence points.

The MaxEnt approach was chosen due to its ability to identify suitable areas of occurrence for species with good predictive power, even for species with small sampling sizes (Elith *et al.*, 2011), while the IDW technique was chosen for providing an alternative hypothesis to niche-based approaches, which can overestimate species distribution prediction to areas beyond the species' dispersal capacity (Diniz-Filho *et al.*, 2003; Pearson and Dawson, 2003; Elith *et al.*, 2011).

#### ▪ Model calibration

Model calibration under current climatic conditions was based on the 19 bioclimatic variables available from the CHELSA database v2.1 (Karger *et al.*, 2021; Appendix 2; Table A2), which represent the mean values of the monthly climate data over the period from 1981 to 2011 (30-year period) as recommended by the World Meteorological Organization (<https://public.wmo.int/>). Bioclimatic variables that were multicollinear and showed a low contribution to explain species distribution models were removed with the aid of the R packages “usdm” (Naimi *et al.*, 2014) and “SDMtune” (Vignali *et al.*, 2020) to avoid noisy information and the overfitting of MaxEnt models. Only variables with low variance inflation factor ( $VIF < 10$ ) and a relative contribution higher than 5% (determined by a jackknife test) were used.

#### 5.2.2. Impact of climate change on the distribution of desiccation-tolerant vascular plants

To assess how climate change may affect DT plants' distribution, the area of the distribution hypothesis of each species in the present was compared with their estimated areas of occurrence under different climate change scenarios. For that, a species distribution hypothesis as described above (i.e., consensus between MaxEnt and IDW models) was generated, but projecting the species distribution under the Coupled Model Intercomparison Project Phase 6 framework (Coupled Model Intercomparison Project, 2025) after calibrating the models with current climatic conditions. Two global climate models under the context of climate change were used: GFDL-ESM4.1 (Dunne *et al.*, 2020), which has a lower equilibrium climate sensitivity, and UKESM1 (Sellar *et al.*, 2019), which has a higher equilibrium climate sensitivity (equilibrium climate sensitivity of 3.4 and 5.4 K, respectively). From those global climate models, climate datasets corresponding to two distinct shared socioeconomic pathways were used. One reflects a more optimistic scenario (SSP1, sustainable path, with environmental boundaries, low greenhouse gas emission) and the other reflects a more pessimistic scenario (SSP5, very high greenhouse gas, with fossil-fueled development). Three future time-series were considered for the years 2011-2040, 2041-2070, and 2071-2100.

### **5.2.3. Impact of climate change on the diversity patterns of desiccation-tolerant vascular plants**

To assess how climate change may affect DT plants' diversity patterns, the current centers of diversity and endemism of DT plants in West Africa were first identified and then re-estimated using the species distribution hypotheses under different climate change scenarios. The centers of diversity were based on species richness, while the centers of endemism were based on endemism richness.

#### **- *Species richness estimation***

To estimate the species richness, the distribution hypotheses of every species were overlapped, and the number of species was counted per spatial unit (i.e., grids of 2°30" x 2°30"). The same weight was attributed to every species to calculate the species richness (i.e., every species counted as 1). Regions with a higher number of species scored a higher species richness.

#### **- *Species endemism estimation***

To estimate the endemism richness, the distribution hypotheses of every species were overlapped, but unlike for species richness, a different weight was attributed to each species before counting the number of species per spatial unit. The weight for each species was calculated based on its inverse range size (i.e., calculated as 1 over the number of grid cells the species is found; **Kier *et al.*, 2009**). The absolute values of the log-transformed scores were used to reduce the effect of the fine spatial resolution, which produced a strong lognormal distribution of endemism richness scores. By this method, a higher contribution of species with a smaller distribution range was given to identify the centers of endemism for DT plants in West Africa. Regions with a higher number of geographically restricted species scored a higher endemism richness.

Those approaches were chosen because, although focusing on a taxonomic perspective, they offer alternative views when considering whether or not species have a more restricted distribution range. Then, the same routine was repeated, but using the species distribution hypothesis for each future scenario.

## **5.3 Investigation of the influence of soil variables on the intraspecific variation in desiccation-tolerant Plants' ecological strategies**

### **5.3.1. Study system and sampled species**

#### **5.3.1.1. Choice of the sampled species**

Four DT grasses known to inhabit rock outcrops such: *Microchloa indica* (L.f.) P.Beauv., *Tripogonella minima* (A.Rich.) Hochst. ex Steud and *Sporobolus festinus* Hochst. ex A. Rich. from the family of Poaceae and *Afrotrilepis pilosa* (Boeck.) J. Raynal from Cyperaceae were identified as this study model species. *Tripogonella minima*, *Sporobolus festinus*, and *Afrotrilepis pilosa* a

perennials, whereas *Microchloa indica* is an annual, and thus two contrasting life history strategies that could help explore intra-specific variation in their ecological strategies could be analyzed. Their native occurrence in seasonally dry ecosystems and known ability to recover from vegetative desiccation under natural conditions (**Farrant and Moore, 2011**) further support their ecological relevance. These attributes position them as informative models to investigate the role of soil characteristics in describing intra-specific variation in ecological strategies among DT plants under environmental stress.

#### **5.3.1.2. Species data collection**

The species specimens were first identified in the field by a botanist, and after which harvesting was conducted from July to October 2023, in the central, northern, and northwestern regions of Côte d'Ivoire, including: Korhogo, Niangbo, Seguela, Silakoro, Dabakala, Bouake and Kokumbo (Figure 14). These localities experience a Sudanian-Guinean tropical climate, characterized by a rainy season from May to October with annual precipitation ranging from 1.200 to 1.400 mm, followed by a dry season from November to April. The dry season is strongly influenced by the Harmattan winds, which typically occur from December to February. The study sites consist of inselbergs, characterized by shallow soils, exposed rock surfaces and pronounced seasonal climatic variation. These features make the inselbergs an ecologically significant model system for investigating desiccation-tolerant plants. The individuals' samples were collected from different sites, considering the specimen, without damage. The samples were collected fresh in boxes and transported to the laboratory, where they were cleaned and conserved in silica gel to avoid damaging them. Leaves were collected from robust, well-grown plants in their habitats, avoiding senescent or damaged leaves.

#### **5.3.2. Sampling design**

The sampling followed the technic described by **Chandran *et al.* (2010)** for vegetation studies. Given the steepness of the study areas, quadrats measuring  $10 \times 10$  m were randomly placed, ensuring a minimum distance of 10 m between plots (Figure 15). Heterogeneity was covered as much as possible, placing the plots in different parts of the rock. even though the areas surveyed were strongly constrained by their accessibility. Within each  $10 \times 10$  m quadrat, five  $1 \times 1$  m plots were established: four located at diagonally opposite corners and one in the center. Species sampling was conducted within these  $1 \times 1$  m plots. The latter dimension was used in accordance with established protocols for sampling herbaceous vegetation and small shrubs (**Chandran *et al.*, 2010**). This scale provides a balance between spatial resolution and sampling efficiency, thereby facilitating precise quantification of species composition and abundance under the challenging conditions of steep terrain. For each plot, the number of species and individuals was recorded. Individuals and soil samples were collected

only for the four target species (Figure 15). Sampling plots within the rock outcrop environments were randomly selected, knowing that on rock you can have plots without soil (Figure 16), those have been excluded. So, only plots where the target species had been collected (could be one species or all of them in the same plot) with soil had been considered in order to link the strategies of species and soil nutrients. Each plot had been treated as an independent unit for data collection. GPS coordinates were recorded for every quadrat. Fresh plant specimens were placed in nursery bags and transported in insulated containers to prevent wilting. Soil samples were taken from the exact location of each plant, placed in labeled envelopes indicating the locality, plot number and coordinates. In the laboratory, plant specimens were cleaned, wrapped, pressed and placed in contact with silica gel to ensure complete preservation.

### 5.3.3. Functional traits measurement

For each plot, three (for big leaves) to ten leaves (for small leaves) from individual plants of the target species were selected. At least 20 individuals were considered for each species, and geographic diversity was ensured by collecting from widely spread sites within the survey area. But for *Afrotrilepis pilosa*, 18 individuals were considered, because most of the plots where that species occurred were without soil. Following collection, the leaves were placed between damp papers, sealed in plastic bags and kept overnight in a dark place. Leaf fresh weight (LFW) was measured from these saturated organs using an analytical weight scale (..... 0.0001 g). The leaves were then flattened and digitized with a CanoScan 9000F scanner to obtain the leaf area (LA). The leaves were then placed in envelopes and put into a drying oven at 60 °C for 72 h, after which leaf dry weight (LDW) was measured. This was used to calculate SLA and LDMC. Leaf traits such as leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), and soil nutrient levels are used as they can provide valuable information about a plant species' environmental adaptation and growth strategy (Figure 17). The leaf area (LA), which refers to the total surface area of a leaf, was measured by scanning leaves (per species), and LA was calculated using ImageJ (**Schneider *et al.*, 2012**). LA is used because it indicates the potential for photosynthesis and resource acquisition; species with larger leaf areas can intercept more sunlight, outcompeting other plants for light resources. Specific leaf area (SLA) is the ratio of leaf area to leaf dry mass, associated with the resource use efficiency. The following formula was used: **SLA = LA/LDW**.

Leaf dry matter content (LDMC) represents the ratio of leaf dry mass to its fresh mass. Species with high LDMC often exhibit stress-tolerant strategies, as denser leaves can help conserve water in arid or stressful environments. It was calculated using the formula: **LDMC (%) = (LDW/LFW) × 100**. The SLA and LDMC were calculated according to the formula used by **Pierce *et al.* (2017)**.

They provide information about plant growing strategy as they are linked to resource acquisition or conservation (**Garnier *et al.*, 2004**). These traits were chosen for their relevance to plant growing strategy in grasslands. Then, the functional traits LA, SLA, and LDMC were assessed then were used later for the strategy tool to calculate species affinities for C-selection, S-selection, and R-selection of the CSR scheme.

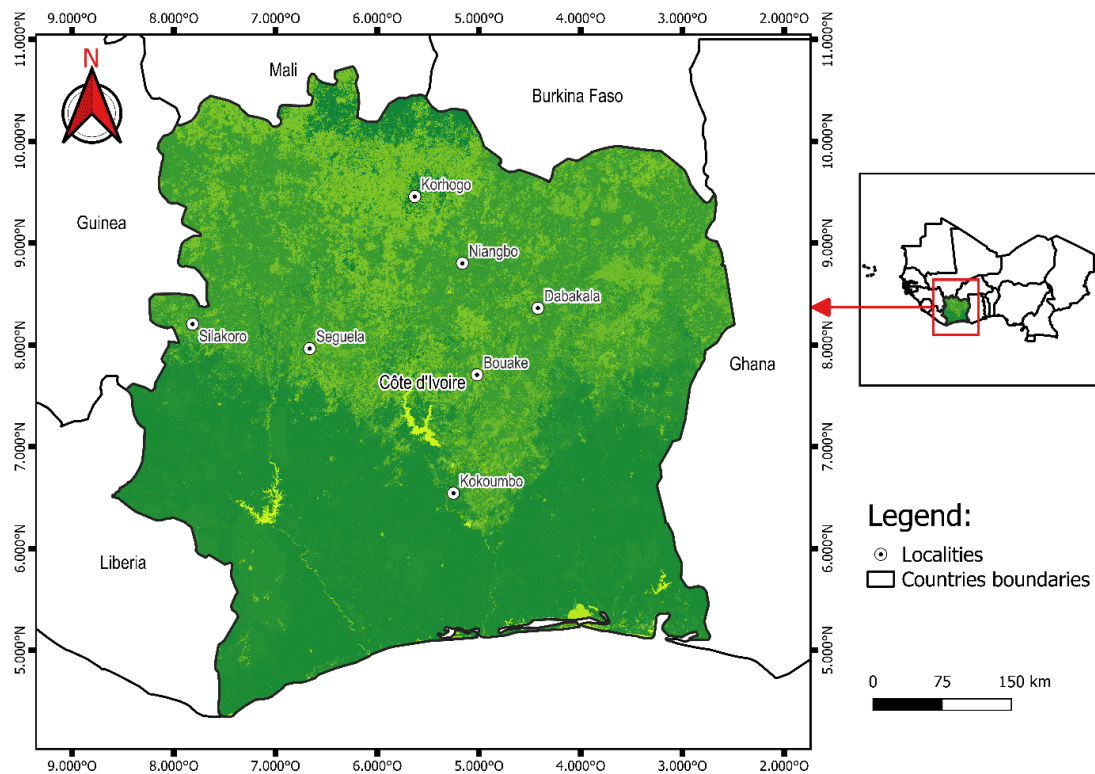
#### **5.3.4. Soil variables measurement**

The physical and chemical properties of the soil, including total nitrogen (N), available phosphorus (P), exchangeable potassium (K), organic carbon (OC), cation exchange capacity (CEC), pH, moisture content, texture and clay percentage, were determined using the AgroCares scanner, a portable device designed to deliver rapid and accurate assessments of soil fertility parameters (**Gregory, 2022**). Before analysis, soil samples were air-dried, finely ground and sieved to obtain a uniform powder suitable for spectroscopic examination. The AgroCares scanner operates on the principle of near-infrared reflectance spectroscopy (NIRS), a non-destructive analytical technique that involves exposing samples to near-infrared (NIR) radiation. Soil constituents selectively absorb this radiation at characteristic wavelengths, enabling the identification and quantification of various soil parameters (**Pansu and Gautheyrou, 2006**). The reflected spectral signals are captured and processed via the AgroCares software, which applies pre-calibrated predictive models to estimate the concentrations of nutrients and other properties, including nitrogen, phosphorus, potassium, organic carbon, CEC, pH, moisture, texture and clay content. Although clay is a component of soil texture, its quantitative value (%) is often reported independently due to its pivotal role in determining key soil functions such as water retention capacity and cation exchange potential.

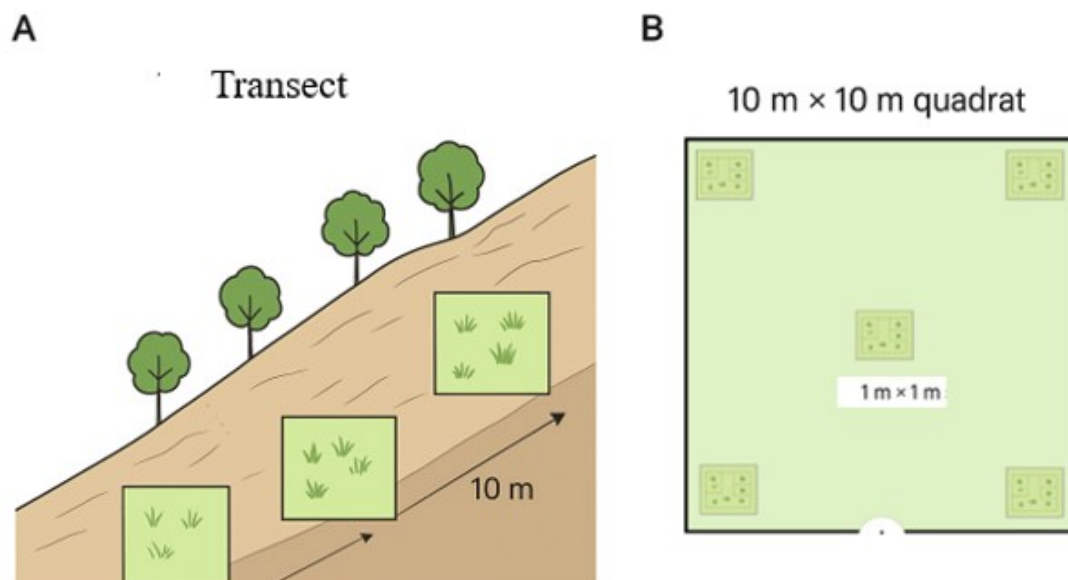
In this study, organic matter (OM) content was used instead of directly measured organic carbon. Although OC is a precise chemical measurement of the carbon component within soil organic materials, OM provides a broader representation of the total organic constituents. The choice of using OM was based on its broader interpretative value in assessing soil quality and biological activity. The OM values were estimated from OC concentrations using the standard conversion factor:

**OM = OC × 1.72**, proposed by **Van Bemmelen (1890)**, based on the assumption that organic matter contains approximately 58% carbon.

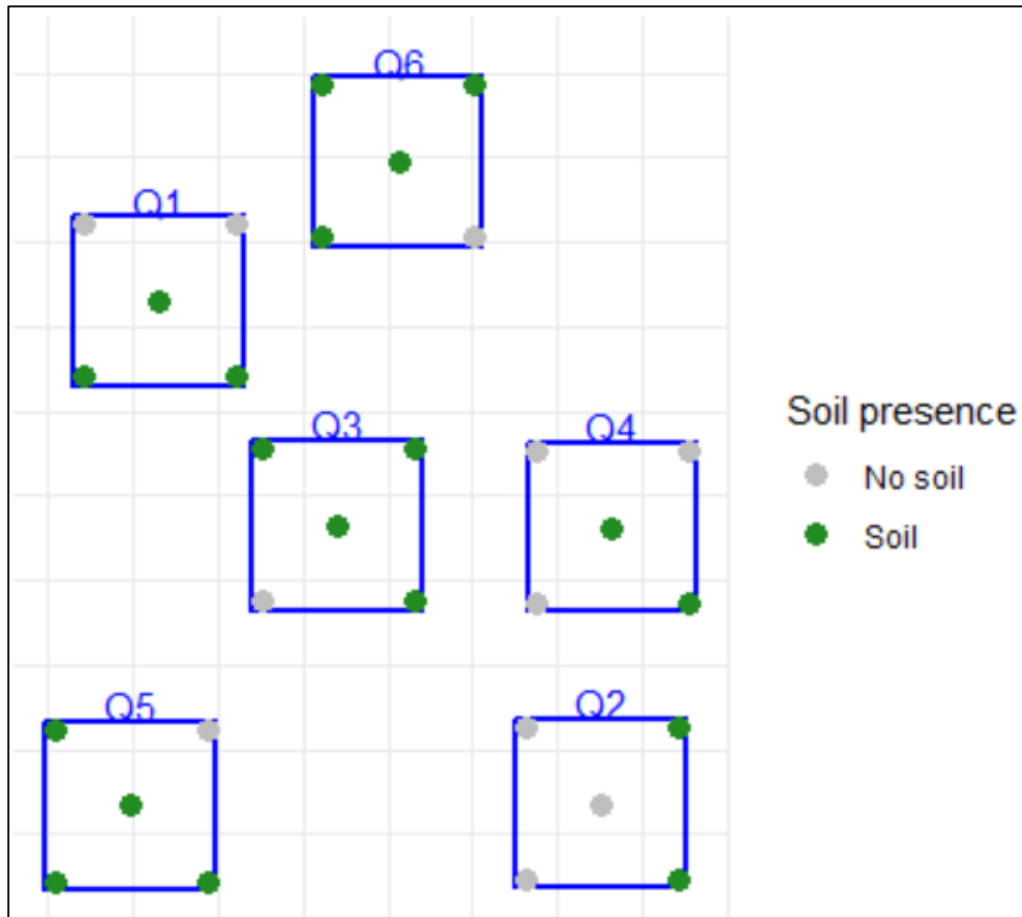




**Figure 14.** Map of the sampled locations in Côte d'Ivoire



**Figure 15.** Species sampling design on inselbergs. **A)** Typical transect showing the quadrats of 10 m × 10 m for trees and shrubs; **B)** Quadrat containing the 5 plots of 1 m × 1 m for the herb layer



**Figure 16.** Experimental design showing the distribution of plots and soil sampling points on inselbergs.

**A**



**B**



**C**



**Figure 17.** Leaf trait measurement techniques and equipment. **A.** CanoScan scanner used to obtain digitized leaf area; **B.** Analytical balance used to weigh leaves; **C.** Flattened leaf material.

## 5.4. Investigation of the effects of seed age on desiccation-tolerance in DT plants

### 5.4.1. Study system and seeds data collection

#### 5.4.1.1. Study system

Poaceae was used as this study model species: *Microchloa indica* (L.f.) P.Beauv. and *Tripogonella minima* (A.Rich.) Hochst. ex Steud. These species were selected to represent distinct ecological and life history strategies within DT Poaceae and to explore how desiccation tolerance operates across different developmental stages (perennial and annual), contributing to a broader understanding of desiccation-tolerance evolution and function in grasses.

Desiccation tolerance is more common in certain lineages within Poaceae (**Gaff and Oliver, 2013; VanBuren, 2017**). Phylogenetically, both *Tripogonella* and *Microchloa* belong to early-diverging lineages in which multiple desiccation-tolerant plants have been identified (**Oliver *et al.*, 2020**), making them valuable for comparative studies. *Tripogonella minima* is a perennial hemicryptophyte and *Microchloa indica*, a loosely caespitose annual; two contrasting life history strategies that could help explore different ecological and developmental expressions of desiccation-tolerance. Their native occurrence in seasonally dry ecosystems and known ability to recover from vegetative desiccation under natural conditions (**Farrant and Moore, 2011**) further support their ecological relevance. These attributes position them as informative models to investigate how desiccation tolerance is expressed during early seedling developmental stages under real environmental stress.

*Tripogonella minima* is a small, slender, caespitose perennial native to Africa. It typically inhabits seasonally dry tropical biomes, including rock outcrops, open grasslands and exposed slopes at elevations ranging from 90 to 1700 m. This species is known for its ability to grow in shallow soils and xeric microhabitats, and is considered one of the more robust desiccation-tolerant grasses of African rock outcrops.

*Microchloa indica* is a loosely caespitose annual or short-lived perennial, native to the Tropical and Subtropical Old World, including parts of northern Australia. It occurs in open grasslands, mopane woodlands, and disturbed habitats such as roadsides and termitaria, from 610 to 2350 m in elevation. Adapted to drought-prone environments, often germinating quickly to exploit transient moisture availability.

#### 4.4.1.2. Seeds collection

Seeds of *Tripogonella minima* and *Microchloa indica* were harvested between October and November 2022 and between October and November 2023 on Mount Korhogo (9.45°N, 5.65°W), located in northern Côte d'Ivoire (Figure 18). The region experiences a Sudanian-Guinean tropical

climate, with a rainy season from May to October (1.200-1.400 mm/year) and a dry season from November to April, strongly influenced by Harmattan winds. Mount Korhogo is a granitic inselberg rising from the surrounding savanna landscape, characterized by shallow soils, exposed rock surfaces, and marked seasonal climatic variation, making it an ecologically relevant model system for studying desiccation-tolerant plants.

#### **5.4.2. Assessment of exposure of *Microchloa indica* and *Tripogonella minima* to drought under climate change**

To investigate the exposure of *Microchloa indica* and *Tripogonella minima* to drought owing to climate change, the Standardized Precipitation Evapotranspiration Index (SPEI; **Vicente-Serrano *et al.*, 2010**) was used. For that, their occurrence records were retrieved from the databases Global Biodiversity Information Facility (**GBIF, 2024**) and Tropicos (**Tropicos, 2024**). Only occurrences within the species' native distribution range according to Plants of the World Online (**POWO, 2022**) were accepted. Duplicated records and erroneous or uncertain data using the R package 'CoordinateCleaner' (**Zizka *et al.*, 2019**) were removed. Records in which the precise description of locality or municipality was provided, were accepted, using the geographic coordinates of the locality or the centroid of the municipality with the aid of the R package 'ggmap' (**Kahle and Wickham, 2013**). Then, the dataset *spei01* was retrieved (i.e., of the monthly temporal scale) from the SPEI database (**Vicente-Serrano *et al.*, 2010**), and the historical records were used for the period from January 1970 to December 2022 (with a 0° 30' x 0° 30' grid cell resolution) for each species' occurrence point.

The SPEI was chosen for being a metric that allows the comparison between locations while considering the multiscalar aspect of drought (i.e., where shorter time scales are mainly related to soil moisture) from the perspective of a hydrological balance (i.e., taking into account the potential evapotranspiration and precipitation for a given location in a given month; **Vicente-Serrano *et al.*, 2010**; **Slette *et al.*, 2019**).

The Mann-Kendall trend test was chosen because it is a method able to identify a monotonic trend in a timeseries, while considering the non-independence and variability of time series data (**Helsel *et al.*, 1993**; **Pohlert, 2016**).

#### **5.4.3. Seed treatments and storage**

Seeds were stored for five different durations post-harvest: 0, 3, 6, 12, 15, and 18 months. Before storage, seeds were manually cleaned and their hulls were removed, then stored in labeled, small, sterile boxes placed inside large airtight glass jars containing silica gel to maintain low humidity and prevent spoilage. All seeds were stored at room temperature (~22-25°C) in a dark, dry environment.

#### 5.4.4. Seedling stage characterization

The experimentation was conducted under a laminar flow cabinet (Thermo Scientific, HeraSafe). Twenty-five (25) seeds were placed into sterile Eppendorf tubes and immersed in 1.5 ml of sodium hypochlorite for up to 2 minutes.

To ensure surface sterilization, the tubes were vortexed (VWR, Vortex VV3), rinsed three times with sterile distilled water. Then, seeds were transferred into 9 cm Petri dishes (Greiner) filled with autoclaved filter paper. Each dish received either 5 ml of distilled water along with 4 ml of natamycin solution to suppress microbial contamination. Dishes were incubated in a climate-controlled growth chamber (Plant Climatics, CLF, model SE-41L) set to a 12 h light/12 h dark cycle, 60–64% relative humidity, with temperatures of 25°C (day) and 21°C (night), and a photon flux density of approximately 260  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Seeds on filter paper were kept consistently moist.

#### 5.4.5. Effect of seed age on desiccation-tolerance

To assess the age effect on desiccation-tolerance ability, seeds of *Tripogonella minima* and *Microchloa indica* were utilized with two differing ages: one batch being 18 months old and the other 6 months old. Sodium hypochlorite (1.5% as concentration) was used for 2 minutes to disinfect seeds to limit contamination. Once the hypocotyl emerged, seedling development was tracked by documenting and taking pictures of the appearance and progression of structures such as leaves, radicles and roots (Figures 48 and 49).

Observations were made under a stereo microscope using an image analysis software to support the identification of morphological traits (Table II), which were used to classify seedling stages. Observations with relevant literature (Tillich, 2007) were combined to characterize post-germination growth and define distinct seedling stages. Each of the eight developmental stages required approximately 150 seedlings. To achieve this, only the germinated seeds were tracked and counted according to their developmental stage. Once the seedlings reached the desired stage, they were transferred and pooled into separate petri dishes corresponding to their respective stage.

To test the hypothesis that the desiccation tolerance capacity of seedlings at different developmental stages decreases with increasing seed age, 7-8 stages were defined (Table II, Figure 48). For *Tripogonella minima*, however, only stages till 7 were taken into account because this species could not grow further in the controlled conditions (Figure 49).

To desiccate the seedlings, for each species, 150 seedlings were dehydrated under a laminar flow cabinet to avoid contamination. The excess water was removed from the petri dishes, and when the filter paper was completely dry (10-15 minutes), the petri dishes were closed and put back in the

climatic chamber for 5 days. After 5 days' dehydration, the seedlings were rehydrated with sterile distilled water, waited for 3 days, and then the number of seedlings that survived and grew further was counted. In some cases, the primary proxy for survival - further development - could not be applied to all stages, since growth potential decreases with seedling age (**Hanley *et al.*, 2004**). Instead, the TTC-method (2,3,5-triphenyltetrazolium chloride) was applied to discriminate between dead and living tissue. If the tissue is alive (Figure 19), the TTC would be coloring it pink. For that, rehydrated seedlings of stages 7-8 were watered with 4ml of 0.5% (w/V) TTC, then incubated in the oven at 30°C for 24h in complete darkness. After this, the seedlings were rinsed 3 times to remove the remaining TTC, and the tissues were examined under a stereo microscope and photographed with a microscope camera (Leica Flexacam i5).

## **5.5. Statistical analyses**

### **5.5.1. Conservation assessment of desiccation-tolerant plants in West Africa**

The conservation status of all identified DT plant species was assessed using the IUCN Red List of Threatened Species version 2025-1 (IUCN,2025). Species were classified into the nine IUCN Red List categories. The categories (i) extinct and (ii) extinct in the wild indicate species are either extinct or only have individuals living outside their natural habitat. Species threatened with extinction are found in the categories (iii) critically endangered, (iv) endangered, and (v) vulnerable, in which their extinction risk decreases in the order given. Those categorized as (vi) near-threatened and (vii) Least Concern are not considered to be at risk of extinction. At last, a lack of assessment exists for species in the categories (viii) data-deficient and (ix) not evaluated, which have insufficient information for assessment, or simply have not yet been assessed for conservation.

To evaluate the current state of research and discussion about the conservation of DT plants in West Africa, the number of studies that focused on West Africa was calculated, and three questions were raised: (i) Did the study discuss the conservation needs of DT plants? (ii) Did the study produce enough evidence to justify the conservation needs of DT plants? (iii) Did the study propose effective conservation strategies for DT plants? Studies that discussed conservation needs for DT plants were considered if they identified DT plants as vulnerable or as strategic components for biological conservation. Using this method, the study that produced enough evidence to justify the conservation needs of DT plants was considered if it quantitatively measured the vulnerability of species or their relevance to any facet of diversity in the ecological contexts they occur (i.e., either taxonomic, phylogenetic, or functional diversity). For the third question, this study, which proposed effective conservation strategies for DT plants, was considered to determine if it suggested, for example, priority species or locations for conservation. To improve the understanding of patterns among those

studies, the studies were grouped in three categories: (1) studies focusing on the entire community, (2) studies focusing on specific community components, and (3) studies focusing on ecological processes and functioning. While in the first group studies that focus on the diversity and ecological patterns of the whole community were included, in the second group, studies in which such patterns are discussed from the perspective of particular habitat types or taxonomic/functional groups are the one who have been included. Lastly, in the third group of studies were included those whose main objective was to discuss the ecological phenomena that explain how community patterns come about, either focusing on the whole community or specific community components.

#### **5.5.2. Exposure to anthropogenic drivers' comparisons.**

To compare DT plants' exposure to quarrying and climate change across unprotected and protected areas, the exposure values for the inselbergs each species exists on, were extracted, then performed a t-test was performed when the data was normally distributed and homoscedastic (in the case of climate change), or a Mann-Whitney U test (in the case of quarrying) when the data did not satisfy the assumptions of parametric statistics. Since hypothesis tests were repeated to include different climate change scenarios, the p-values were adjusted using the Bonferroni correction.

For the graphics representation purposes, a phylogenetic tree was produced using the phylogenetic hypothesis (as Scenario 3) provided by **Jin and Qian (2019)**. All analyses were conducted and all graphical representations were created using the software R, version R.4.2.2 (**R core team, 2025**, Appendix 2; Table A3 for the used R packages).

#### **5.5.3. Model evaluation and consensus building**

Both MaxEnt and IDW techniques were evaluated by the Area Under the Receiver Operating Characteristic Curve (AUC) and True Skill Statistics (TSS) metrics via a k-fold cross-validation ( $k = 5$ ). Background points were randomly generated according to the number of occurrence records. For this, the following points were used:

- 100 for species with records  $< 100$
- 1000 for species with records comprised within 100-300, and
- 10,000 for species with records  $> 300$  (**Barbet-Massin *et al.*, 2012**).

The final distribution hypothesis of species was produced by the agreement between the binary output (i.e., presence-absence predictions); each model was produced using the individual model's thresholds, minimizing omission rates for true positives and true negatives (i.e., best sensitivity and specificity). Each MaxEnt and IDW distribution hypothesis was generated from the 50% consensus

across five modelling routines (including different random cross-validation), for a minimum score of 0.8 for AUC and 0.6 for TSS achieved.

#### **5.5.4. Quantifying the impact of climate change on desiccation-tolerant plants species distribution area in West Africa**

To estimate the direct impact of climate change on their distribution, the area of species distribution hypotheses (in km<sup>2</sup>) was calculated under current and projected climate conditions. For the assessment, in comparison to current distribution areas:

- Reductions in species distribution areas would describe a negative impact of climate change on species by possibly promoting contractions in species' geographical range.
- Increases in species distribution areas (area expansion) would describe a positive impact of climate change on species by possibly favoring expansions in species' geographical range.

The same climatic variables (Table A12, Appendix 13) were used to calibrate the species' current distribution models for future projections of their distribution. Although the IDW technique does not consider the effects of climate change, it was used to generate species distribution hypotheses under climate change to take into account the species' capacity to disperse to new suitable areas. The consensus between the two global climate models (i.e., GFDL-ESM4.1 and UKESM1) was used to facilitate the interpretation of our results, and used contrasting global climate models and shared socioeconomic pathways to obtain a more comprehensive view of the potential impact of climate change on species distribution.

#### **5.5.5. Quantifying the impacts of climate change on species richness and endemism richness**

To assess the impact of climate change on species richness and endemism, their changes per grid cell were quantified.

For species richness:

- Reductions in species richness per spatial unit (i.e., grid cell) would describe a negative impact of climate change by possibly promoting species loss,
- while increases in species richness per spatial unit would describe a positive impact (assuming that higher diversity is positive) of climate change on species by favoring the occurrence of a higher number of species.

For endemism richness, here, changes in endemism richness should be interpreted less straightforwardly.

- While reductions in endemism richness per spatial unit could describe species loss, it could also describe expansions in species climatically suitable areas because the weight of a species



in the index is inversely proportional to its geographical range (i.e., increases in species climatically suitable areas decrease the contribution of species to endemism richness). The opposite is also true.

- Increases in endemism richness per spatial unit could describe the gain of species, but it could also describe reductions in species' climatically suitable areas. Although the existence of important constraints to species distribution in smaller scales was recognized in this study (e.g., biotic interactions and stochasticity; **Peason and Dawson, 2003**), they were not taken into account.

Jenks' natural breaks optimization was used to create 5 different interval classes for diversity patterns (Table A11, Appendix 3), from both taxonomic and endemism perspectives, recognizing areas of low, very low, moderate, high, and very high species or endemism richness. So, regarding the centers of diversity for DT plants, locations were classified based on species as follows: very low diversity (species richness ranging from 1 to 2 species), low diversity (species richness ranging from 3 to 5 species), moderated diversity (species richness ranging from 6 to 11 species), high diversity (species richness ranging from 12 to 26 species), and very high diversity (species richness ranging from 27 to 28 species). Centers of diversity and endemism, the regions with high or very high species and endemism richness, were considered respectively.

For all the spatial and statistical analyses, R 4.4.2 software (**R Core Team, 2024**) and the R package "terra" (**Hijmans, 2023**) were used to conduct our modeling routines and the R packages "ggplot2" (**Wickham, 2016**), "sf" (**Pebesma, 2018**), "rnatualearth" (**South, 2017**), "BAMMtools" (**Rabosky et al., 2014**), and "viridis" (**Garnier et al., 2021**) to generate our graphical representations (Table A11, Appendix 3).

#### 5.5.6. Functional strategy classification

To estimate species ecological strategies following Grime's CSR scheme (C-selection: competitiveness, R-selection: ruderalism, and S-selection: stress-tolerance), the analysis of the CSR functional strategy of Grime (**1974, 1977, 2001**) of each of the target species was quantified according to the globally calibrated method of **Pierce et al. (2017)**, implemented in the "StrateFy" tool. StrateFy was used to calculate the relative proportions of CSR strategies for each species based on their SLA, LDMC, and LA values (**Pierce et al., 2017**) and was plotted in a **ternary diagram** to visualize ecological strategy patterns. Colors of species points were assigned based on RGB transformations of C–S–R ratios (secondary CSR strategy classes suggested by Grime, 2001), where red represents **competitiveness**, green represents **stress-tolerance**, and blue represents **ruderalism** (**Pierce et al., 2017**).

The percentage values of the C, S, and R components for each sample were used to compute the mean values of each component across all individuals in the dataset and the resulting average functional signature of the species, indicating its general ecological position. These averages were interpreted to assess whether the species exhibited a specialized (e.g., strongly stress-tolerant) or generalized (e.g., mixed CSR) strategy. Strategy classes were grouped into categories based on their type: Pure strategies (C, S, R) and intermediate or mixed strategies (e.g., C/CSR, CS/CSR, S/SR). This allowed us to evaluate the distribution and dominance of various ecological strategies within each species. To better interpret the ecological meaning of the CSR strategies, the relative importance of the individual traits, leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC) was analyzed in contributing to the C, S, and R dimensions. According to Grime's CSR theory and confirmed by **Pierce *et al.* (2017)**:

- High LA is typically associated with competitive (C) species, which rely on rapid resource acquisition and dominance in productive habitats.
- High LDMC reflects stress-tolerant (S) strategies, indicating investment in structural resilience and conservation of resources under environmental stress.
- High SLA is linked to ruderal (R) strategies, which are adaptive for fast growth and reproduction in disturbed environments.

By examining the trends in these traits alongside the CSR output from “StrateFy”, the observed functional strategies were underpinned by specific physiological adaptations.

#### **5.5.7. Soil-trait relationships**

To identify variables that were highly correlated, potentially redundant, and decide which one to keep for the analysis, pairwise correlations between soil variables were calculated using the Pearson correlation (Figure 20) coefficient ( $r$ ), which measures the strength and direction of linear relationships between variables. The resulting correlation matrix was visualized as a heatmap, with the color scale indicating the magnitude and sign of  $r$ . Highly correlated variables ( $|r| \geq 0.7$  or  $0.8$ ) were considered redundant, and only one variable from each highly correlated pair was retained. Variables retained after this screening were subsequently used in multivariate analyses to explore their influence on intraspecific variation in ecological strategies. Graphics and analyses were done using R software version 4.4.2 (**R core team, 2024**).

#### **5.5.8. Evaluation of species exposure to drought**

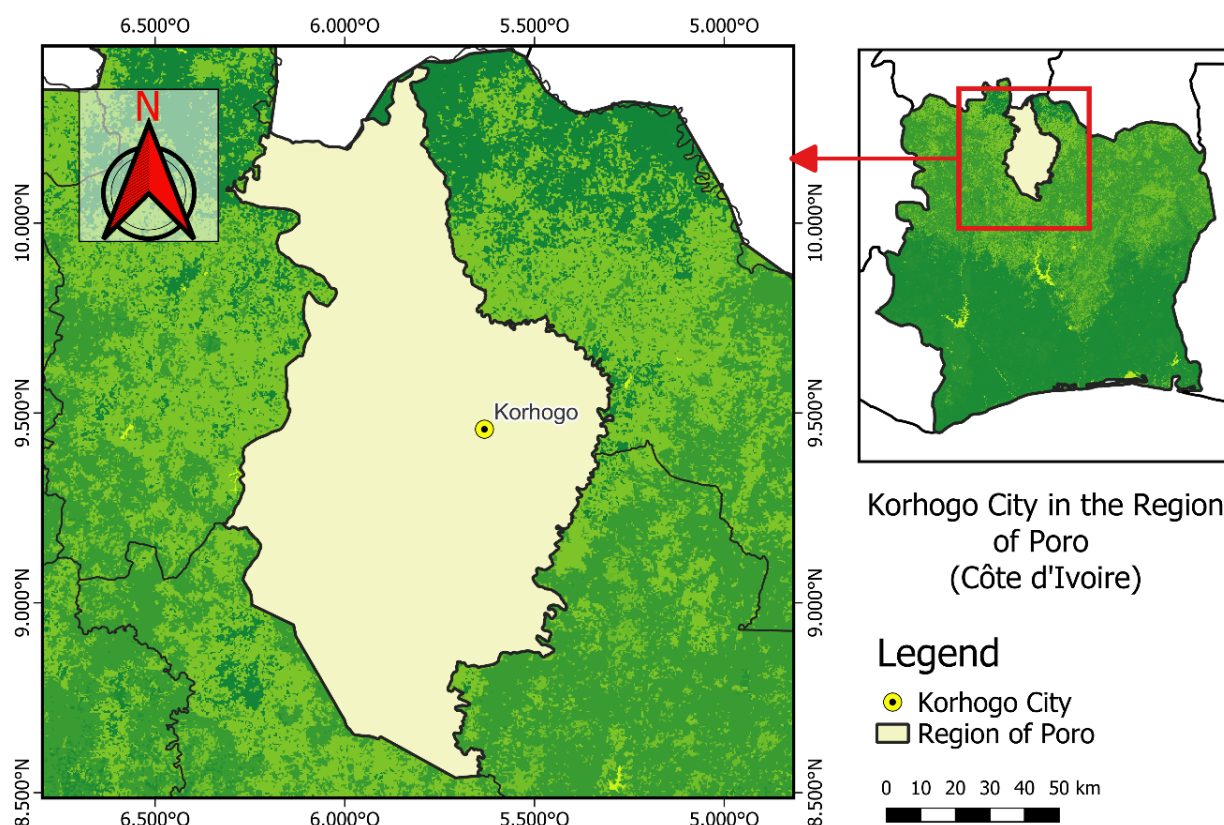
To evaluate trends in species exposure to drought, the mean of the monthly SPEI values was used for all occurrence points for each species, and a Mann-Kendall trend test was used with the aid of the R

package ‘trend’ (Pohlert, 2016). Negative and positive trends are depicted by negative and positive values of Kendall's  $\tau$ , respectively.

Negative SPEI values would describe months in which the evaporative demand surpasses the water supplied by precipitation (i.e., drought), being values lower than  $-1$  describing conditions beyond the range of normal climatic variability. Positive SPEI values would describe months in which such a deficit in water supply is not observed.

#### **5.5.9. Assessment of seed age on desiccation-tolerance**

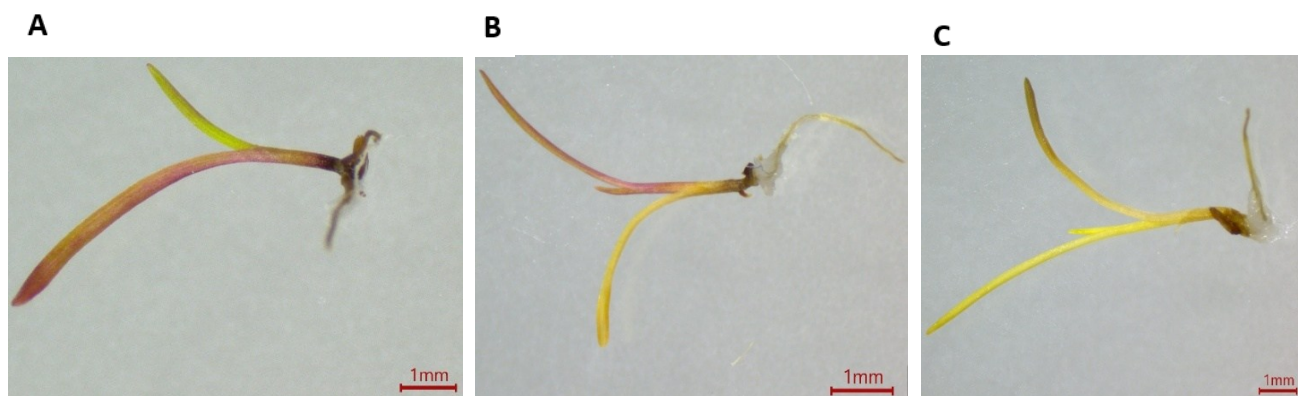
To assess the effect of seed age and development stage on the desiccation-tolerance (percentage of survival), a first logistic linear model was performed. Seed age was categorized into two levels (6 months and 18 months), with 6 months serving as the reference category. The developmental stage was treated as a categorical variable, with stage 1 as the reference level. Stage 1 is chosen as the reference level because it represents the earliest point in seedling development, making it a meaningful starting point. All the analyses and graphical representations were done using the software R, version R.4.2.2.



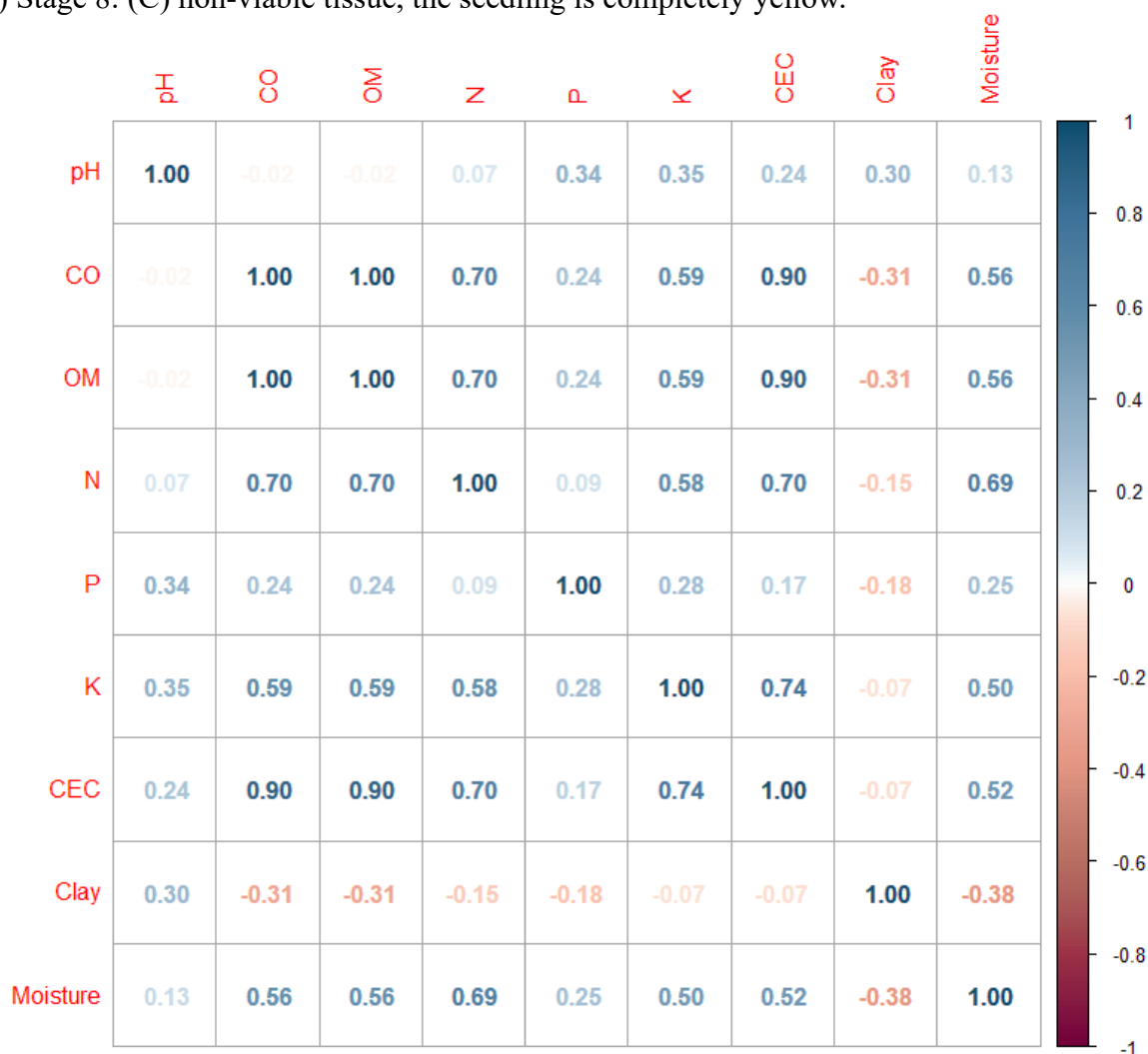
**Figure 18.** Map showing Korhogo as the seed sampling location for *Microchloa indica* and *Tripogonella minima* in Côte d'Ivoire.

**Table II.** Description of the different stages for the two species

| Stage of development | Description                                                               |
|----------------------|---------------------------------------------------------------------------|
| 1                    | Uptake of water, changing in size and shape                               |
| 2                    | Testa rupture                                                             |
| 3                    | Obstruction and appearance of the radicle                                 |
| 4                    | Clearly visible emergence of the coleoptile                               |
| 5                    | Coleoptile and development of the root (violet)                           |
| 6                    | Cotyledon is photosynthetically active (Green), with well developed root. |
| 7                    | Cotyledon well developed                                                  |
| 8                    | Formation of the first leaf, in some cases, a secondary root              |



**Figure 19.** Tissue viability test of *Microchloa indica* using 2,3,5-triphenyltetrazolium chloride (TTC). (A-B) Stage 7: (A) viable tissue stained pink and (B) non-viable tissue remaining unstained/yellow. (C) Stage 8: (C) non-viable tissue, the seedling is completely yellow.



**Figure 20.** Pearson correlation matrix of measured soil physicochemical variables used to identify redundant predictors before soil-trait relationship analyses. The color variation indicating whether the variables are highly/low positively correlated, close/far to the blue, and highly/low negatively correlated, close/far to the red. With: nitrogen (N), phosphorus (P), exchangeable potassium (K), organic carbon (OC), and cation exchange capacity (CEC).

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## **PART THREE : RESULTS AND DISCUSSION**

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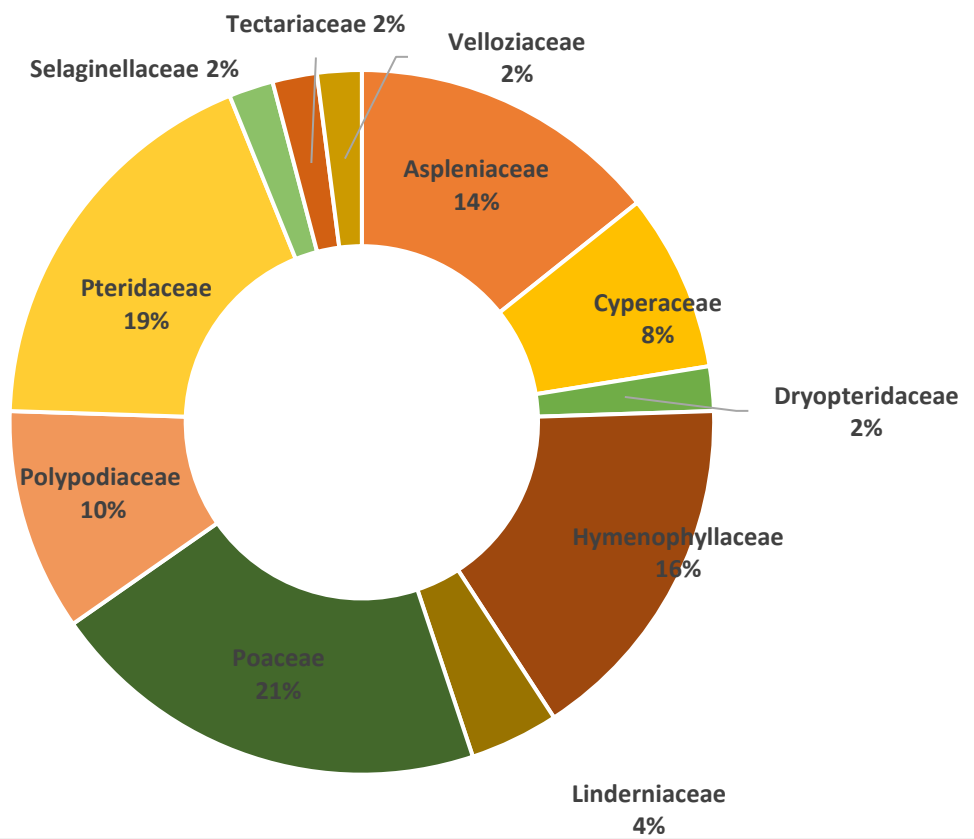
This section is structured into five chapters. Four chapters present the results corresponding to each objective of the thesis, while the final chapter is dedicated to the overall discussion. Specifically, Chapter 6 reports the current state of knowledge and the effectiveness of the existing conservation efforts for desiccation-tolerant plants in West Africa. Chapter 7 assesses the potential impacts of climate change on the distribution and diversity patterns of desiccation-tolerant plants in West Africa. Chapter 8 investigates the role of soil in influencing intraspecific variation in species' ecological strategies, and Chapter 9 investigates how seed ageing affects the desiccation-tolerance in DT plants. Finally, Chapter 10 discusses the main findings of the study.

## **Chapter 6: Diversity, distribution, conservation status and exposure to anthropogenic pressures of DT plants in West Africa**

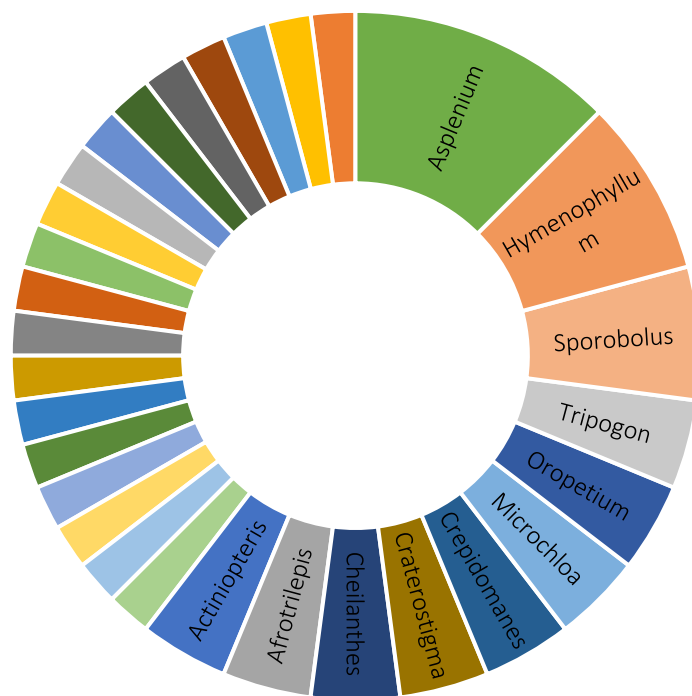
### **6.1. Diversity, distribution and conservation of desiccation-tolerant plants**

Altogether, 49 desiccation-tolerant plant species were found in West Africa and belonging to 30 genera and 11 families across lycophytes, ferns and angiosperms (Table 1). Ferns represented 61.22%, angiosperms 36.73% and lycophytes 2.04% of the species listed. Overall, Poaceae emerged as the most species-rich, with ten species (20.40%), followed by Pteridaceae and Hymenophyllaceae, respectively, with nine (18.36%) and eight (16.32%) species (Figure 21a). Within the genus, *Asplenium* stood out as the most species-rich genus, with six species reported, followed by *Hymenophyllum* and *Sporobolus* with four and three species, respectively (Figure 21b). Within Angiosperm, the findings revealed that out of the four families in which desiccation tolerance occurs in West Africa, three are monocotyledons: Cyperaceae, Poaceae and Velloziaceae. Poaceae is the most diverse, represented by 10 species (20.40% of the total DT species recorded and 55.55% of the angiosperm DT species), distributed across 5 genera (Table III). The family of Cyperaceae follows, representing 10.20% of the overall listed species and 27.77% of the angiosperms, represented by 5 species distributed within three genera. The last monocotyledon's family, Velloziaceae, is represented by a single species, *Xerophyta schnitzleinia*. In contrast, only one family represents dicotyledons in West Africa, Linderniaceae, having one genus, *Craterostigma*, and two species: *Craterostigma plantagineum* and *Craterostigma yaundense* (Table III). Ferns are the most dominant group and represent 61.22% of the species recorded; they are found in six families, with Pteridaceae having 9 species (30% of the ferns), divided into 7 genera; followed by Hymenophyllaceae with 8 species (26.67% of the ferns) and 4 genera, Aspleniaceae with 6 species (20%) and 1 genus, Polypodiaceae with 5 species (16.67% of the ferns) and 5 genera, Diopteridaceae and Tectariaceae represented by only 1 species and 1 genus each (Table 1). Lycophytes are almost absent; they are represented by one family, Selaginellaceae, and have only one species in West Africa: *Selaginella njamnjamensis* Hieron.

A



B



**Figure 21.** Distribution of desiccation-tolerant plants across: (A)- Families and (B)- Genera in West Africa



**Table III.** Checklist of desiccation-tolerant vascular plants present in West Africa, their distribution and conservation status according to the IUCN Red List.

|                                                             | Distribution in West Africa                      | IUCN Red List Categories |
|-------------------------------------------------------------|--------------------------------------------------|--------------------------|
| Lycophytes                                                  |                                                  |                          |
| Selaginellaceae                                             |                                                  |                          |
| <i>Selaginella njamnjamensis</i> Hieron.                    | BEN, CMR, MLI, NGA                               | Not evaluated            |
| Pteridophytes                                               |                                                  |                          |
| Aspleniaceae                                                |                                                  |                          |
| <i>Asplenium aethiopicum</i> (Burm.f.) Becherer             | CIV, CMR, GGN, GIN, GNQ, LBR, NER, NGA, SLE, TCD | Vulnerable               |
| <i>Asplenium friesiorum</i> C.Chr.                          | CMR, GGN, NGA                                    | Not evaluated            |
| <i>Asplenium megalura</i> Hieron.                           | CIV, CMR, GHA, GGN, GIN, LBR, SLE, TGO           | Not evaluated            |
| <i>Asplenium monanthes</i> L.                               | CMR, GGN                                         | Least Concern            |
| <i>Asplenium sandersonii</i> Hook.                          | CMR, GGN, GNQ, NGA                               | Not evaluated            |
| <i>Asplenium stuhlmannii</i> Hieron.                        | CIV, CMR, GIN, NGA, SLE                          | Not evaluated            |
| Dryopteridaceae                                             |                                                  |                          |
| <i>Elaphoglossum acrostichoides</i> (Hook. & Grev.) Schelpe | CIV, CMR, GGN, GHA, GIN, LBR                     | Least Concern            |
| Hymenophyllaceae                                            |                                                  |                          |
| <i>Crepidomanes chevalieri</i> (Christ) Ebihara & Dubuisson | CIV, CMR, GGN, GHA, GIN, LBR, NGA, SLE           | Not evaluated            |
| <i>Crepidomanes melanotrichum</i> (Schltdl.) J.P.Roux       | CIV, CMR, GGN, GHA, GIN, LBR, NGA, SLE           | Not evaluated            |
| <i>Didymoglossum erosum</i> (Willd.) Beentje                | CIV, CMR, GHA, GIN, LBR, NGA, SLE                | Not evaluated            |
| <i>Hymenophyllum capillare</i> Desv.                        | CMR, GGN, GHA                                    | Not evaluated            |
| <i>Hymenophyllum hirsutum</i> (L.) Sw.                      | CMR, GGN, GHA, GIN, GNQ, CIV, LBR                | Not evaluated            |
| <i>Hymenophyllum kuhnii</i> C.Chr.                          | CMR, GGN, GHA, GIN, GNQ, LBR, NGA, SLE           | Not evaluated            |
| <i>Hymenophyllum splendidum</i> Bosch                       | CMR, GNQ                                         | Not evaluated            |

(Continued)

Table III. Continued.

|                                                             |                                                               |               |
|-------------------------------------------------------------|---------------------------------------------------------------|---------------|
| <i>Polyphlebium borbonicum</i> (Bosch) Ebihara & Dubuisson  | CIV, CMR, GGN, GNQ, GH, GIN, LBR                              | Not evaluated |
| Polypodiaceae                                               |                                                               |               |
| <i>Loxogramme abyssinica</i> (Baker) M.G.Price              | CIV, CMR, GGN, GH, GIN, GNQ, LBR, NG, SLE, TGO                | Not evaluated |
| <i>Melpomene flabelliformis</i> (Poir.) A.R.Sm. & R.C.Moran | CMR, GGN                                                      | Not evaluated |
| <i>Phymatosorus scolopendria</i> (Burm.f.) Pic.Serm.        | BEN, CIV, CMR, GGN, GNQ, GH, GIN, LBR, NG, SLE, TGO           | Not evaluated |
| <i>Platyserium stemaria</i> (P.Beauv.) Desv.                | BEN, CIV, CMR, GGN, GNQ, GH, GIN, LBR, NG, SEN, SLE           | Not evaluated |
| <i>Pleopeltis macrocarpa</i> (Willd.) Kaulf.                | CIV, CMR, GGN, GIN, LBR, NG, SLE                              | Not evaluated |
| Pteridaceae                                                 |                                                               |               |
| <i>Actiniopteris radiata</i> (Sw.) Link                     | CMR, CPV, MLI, NG, TCD, TGO                                   | Not evaluated |
| <i>Actiniopteris semiflabellata</i> Pic.Serm.               | MRT                                                           | Not evaluated |
| <i>Adiantum incisum</i> Forssk.                             | CIV, CMR, CPV, GH, NG, TGO                                    | Not evaluated |
| <i>Cheilanthes coriacea</i> Decne.                          | NER, TCD                                                      | Not evaluated |
| <i>Cheilanthes inaequalis</i> Mett.                         | CMR, GIN, NG                                                  | Not evaluated |
| <i>Cosentinia vellea</i> (Aiton) Tod.                       | CPV                                                           | Least Concern |
| <i>Hemionitis farinosa</i> (Forssk.) Christenh.             | CMR, GGN, NG, SLE                                             | Not evaluated |
| <i>Pellaea doniana</i> Hook.                                | GNQ                                                           | Not evaluated |
| <i>Vittaria guineensis</i> Desv.                            | CIV, CMR, GGN, GH, GIN, GNQ, LBR, NG, SLE, TGO                | Not evaluated |
| Tectariaceae                                                |                                                               |               |
| <i>Arthropteris orientalis</i> (J.F.Gmel.) Posth.           | CIV, CMR, GGN, GH, GIN, LBR, NG, SLE                          | Not evaluated |
| Angiosperms                                                 |                                                               |               |
| Cyperaceae                                                  |                                                               |               |
| <i>Afrotrilepis jaegeri</i> J.Raynal                        | SLE *                                                         | Not evaluated |
| <i>Afrotrilepis pilosa</i> (Boeckeler) J.Raynal             | BEN, BFA, CIV, CMR, GH, GIN, GNQ, LBR, MLI, NG, SEN, SLE, TGO | Not evaluated |
| <i>Coleochloa abyssinica</i> (Hochst. ex A.Rich.) Gilly     | CMR, NG                                                       | Not evaluated |

(Continued)

Table III. Continued.

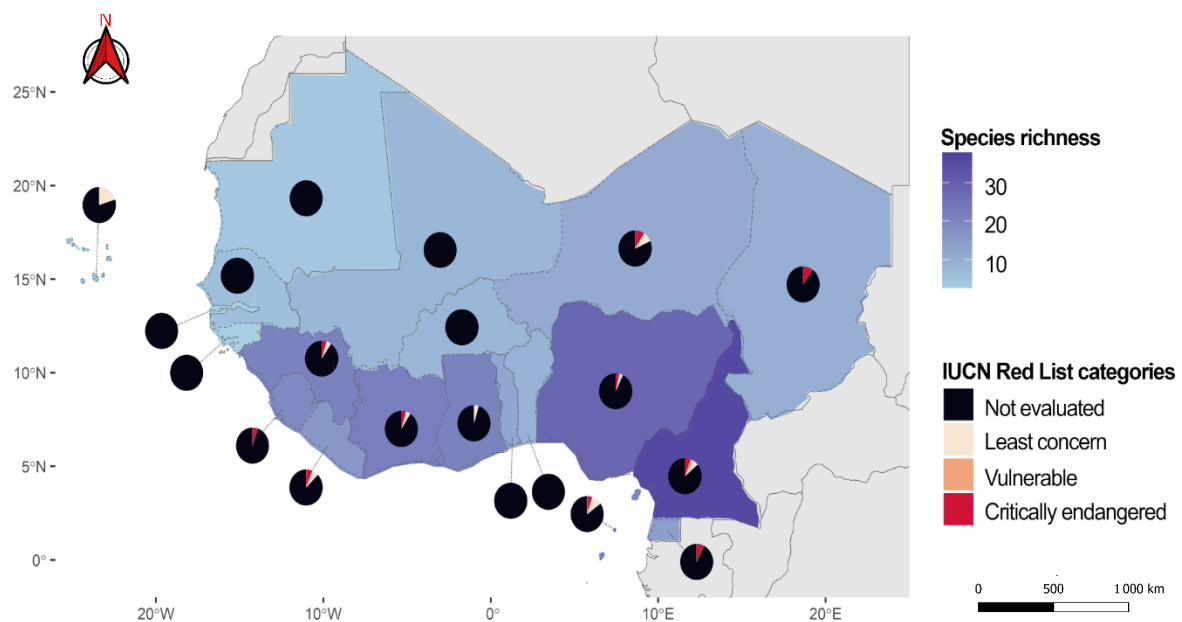
|                                                                           |                                                                           |                       |
|---------------------------------------------------------------------------|---------------------------------------------------------------------------|-----------------------|
| <i>Coleochloa domensis</i> Muasya & D.A.Simpson                           | CMR *                                                                     | Critically endangered |
| <i>Microdracoides squamosa</i> Hua                                        | CMR, GIN, NGA, SLE *                                                      | Not evaluated         |
| Linderniaceae                                                             |                                                                           |                       |
| <i>Craterostigma plantagineum</i> Hochst.                                 | BFA, NER, TCD                                                             | Not evaluated         |
| <i>Craterostigma yaundense</i> (S.Moore) Eb.Fisch., Schäferh. & Kai Müll. | CMR *                                                                     | Vulnerable            |
| Poaceae                                                                   |                                                                           |                       |
| <i>Microchloa indica</i> (L.f.) P.Beauv.                                  | BEN, BFA, CIV, CMR, GHA, GIN, GNB, MLI, NER, NGA, SEN, SLE, TCD, TGO      | Not evaluated         |
| <i>Microchloa kunthii</i> Desv.                                           | BEN, BFA, CIV, CMR, GHA, NGA, TGO                                         | Not evaluated         |
| <i>Oropetium aristatum</i> (Stapf) Pilg.                                  | BEN, BFA, CIV, GHA, GMB, GNB, MLI, NER, SEN, TGO *                        | Not evaluated         |
| <i>Oropetium capense</i> Stapf                                            | MLI, MRT, NER, TCD                                                        | Not evaluated         |
| <i>Sporobolus festivus</i> Hochst. ex A.Rich.                             | BEN, BFA, CIV, CMR, GHA, GIN, GMB, GNQ, MLI, MRT, NER, NGA, SEN, TCD, TGO | Not evaluated         |
| <i>Sporobolus pellucidus</i> Hochst.                                      | BFA, NER, TCD                                                             | Not evaluated         |
| <i>Sporobolus stapfianus</i> Gand.                                        | NER, NGA                                                                  | Least Concern         |
| <i>Tripogon major</i> Hook.f.                                             | SLE                                                                       | Not evaluated         |
| <i>Tripogon multiflorus</i> Miré & H.Gillet                               | CPV, NER, TCD                                                             | Not evaluated         |
| <i>Tripogonella minima</i> (A.Rich.) P.M.Peterson & Romasch.              | BEN, BFA, CIV, CMR, CPV, GHA, MLI, MRT, NER, NGA, SEN, TCD, TGO           | Not evaluated         |
| Velloziaceae                                                              |                                                                           |                       |
| <i>Xerophyta schnitzleinia</i> (Hochst.) Baker                            | NGA, GNQ                                                                  | Not evaluated         |

BEN-Benin; BFA-Burkina Faso; CIV-Côte d'Ivoire; CMR-Cameroon; CPV-Cabo Verde; GGN-Gulf of Guinea Is.; GHA-Ghana; GIN-Guinea; GMB-the Gambia; GNB-Guinea-Bissau; GNQ-Equatorial Guinea; LBR-Liberia; MLI-Mali; MRT-Mauritania; NER-Niger; NGA-Nigeria; SEN-Senegal; SLE-Sierra Leone; TCD-Chad; TGO-Togo.

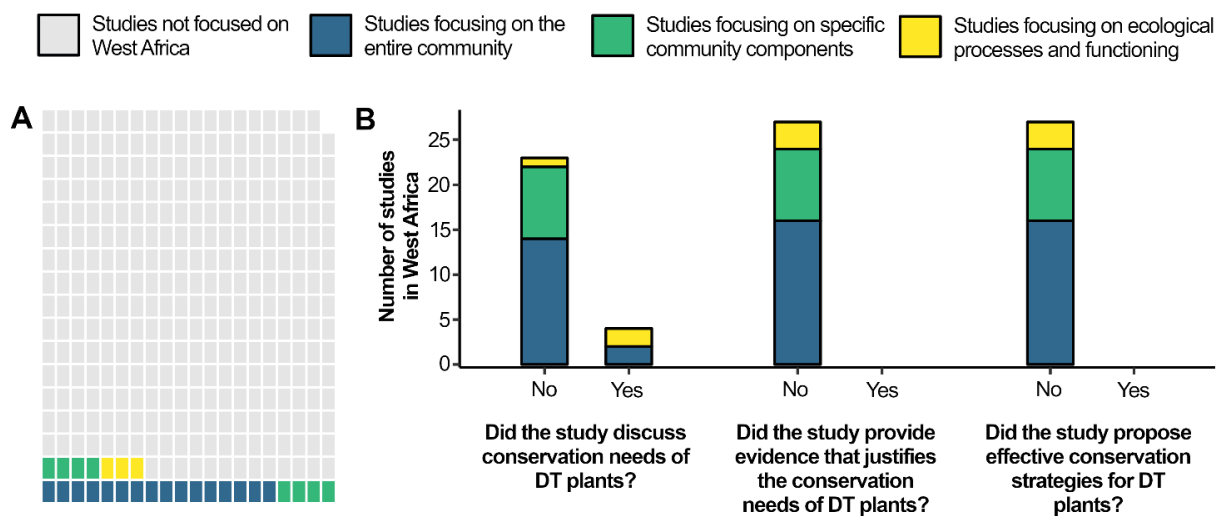
Regarding the distribution of species in West Africa, Cameroon stood out as the country most rich in species (36), followed by Nigeria (28) and Côte d'Ivoire (22; Figure 22). The Gambia and Guinea-Bissau were the countries with the lowest number of species, having two species each. While some species were widespread in West Africa, others were restricted to one or a few countries. *Sporobolus festivus* (Poaceae) was the species most widespread in West Africa, being recorded in 15 countries. On the other hand, certain species were found in only one country in West Africa, including three nationally endemic species: *Afrotrilepis jaegeri* (Cyperaceae), endemic to Sierra Leone, and *Coleochloa domensis* (Cyperaceae) and *Craterostigma yaundense* (Linderniaceae), both endemic to Cameroon.

In total, six species are endemic to West Africa. Besides *Afrotrilepis pilosa*, *A. jaegeri*, *C. domensis*, and *C. yaundense*, *Microdracoides squamosa* (Cyperaceae) and *Oropetium aristatum* (Poaceae) also have their distribution restricted to West Africa. Concerning the conservation status of the DT plants in West Africa, 42 species (86%) of the 49 listed have not been evaluated for conservation by the IUCN. Only seven species (14%) have been evaluated, among which four species were classified as Least Concern (*Asplenium monanthes*, *Elaphoglossum acrostichoides*, *Cosentinia vellea* and *Sporobolus stapfianus*, of the families of Aspleniaceae, Dryopteridaceae, Pteridaceae and Poaceae, respectively), two species as Vulnerable (*Asplenium aethiopicum* and *C. yaundense*, of the families of Aspleniaceae and Linderniaceae, respectively), and one species as Critically endangered (*C. domensis*; Cyperaceae). A complete lack of assessment of DT plants for conservation was registered in eight countries in West Africa (40%). While 12 countries (60%) have at least one species assessed by IUCN, most species in those countries have not yet been assessed concerning their conservation.

Out of the 339 studies, only 27 studies (7.9%) were focused on West Africa (Figure 23; Appendix 2; Table A4). Most of these 27 studies were focused on the entire community in which DT plants are embedded (16 studies, 4.7%). Eight studies focused on specific community components (2.3%), while only three studies focused on ecological processes and functioning (0.8%). Among those studies (Appendix 2, Table A4), only four (1.2% of studies, or 15% of studies on DT plants of West Africa) mentioned the conservation needs of DT plants (**Porembski et al., 2016; Porembski, 2007; Porembski, 2000; Porembski et al., 1994**), although no studies either produced enough evidence to justify the conservation needs of DT plants or proposed effective conservation strategies for DT plants. Of these four studies that mentioned the conservation needs about DT plants, two focused on the entire community (**Porembski 2007; Porembski et al., 1994**) and two focused on the ecological processes and functioning (**Porembski et al., 2016; Porembski, 2000**) of the DT plants that have been found in an ecological context.



**Figure 22.** Number of desiccation-tolerant vascular plant species in West Africa per country (species richness) and their conservation status according to IUCN Red List categories.

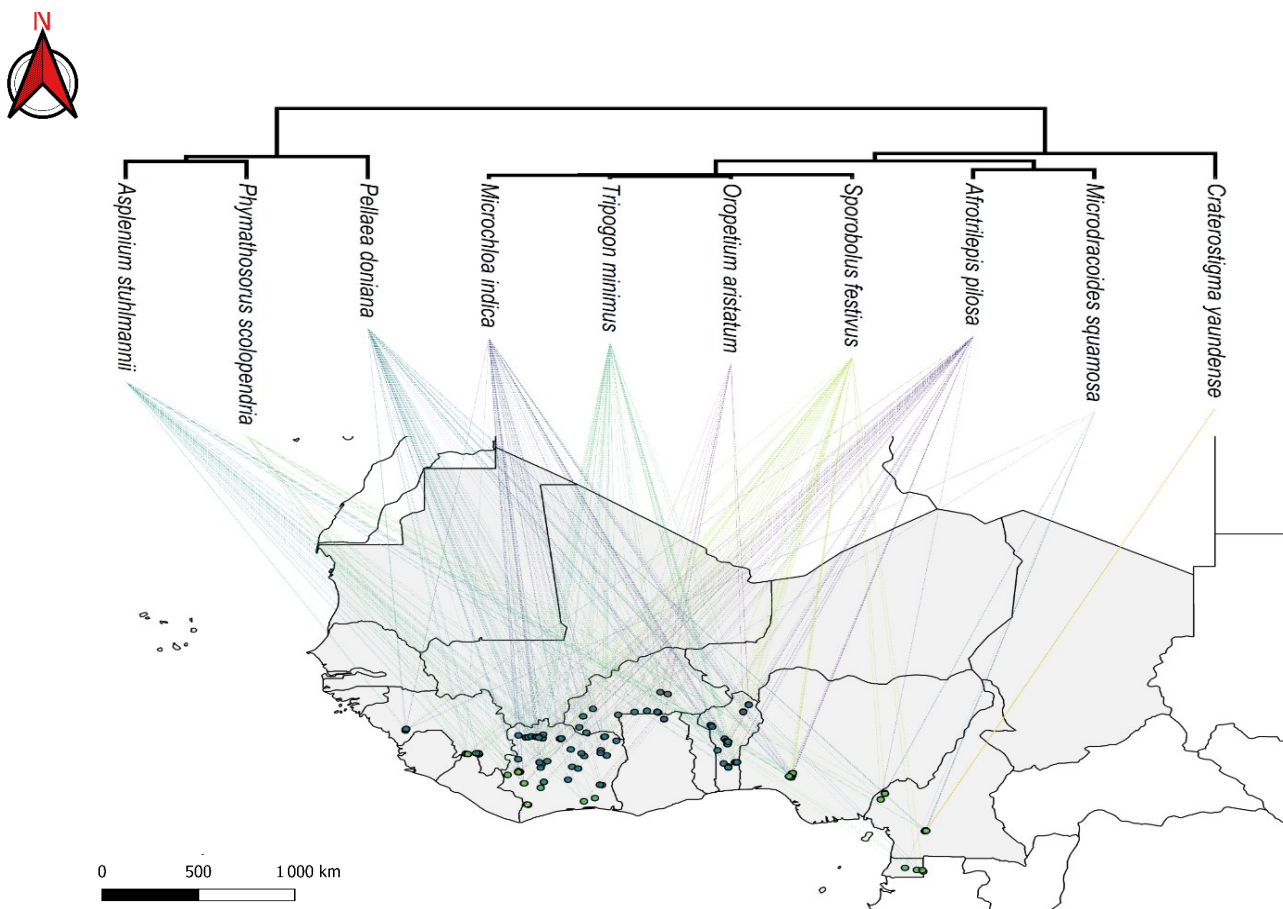


**Figure 23.** The number of studies on desiccation-tolerant vascular plants selected in our systematic review by 3 established categories. (A)—number of studies with explicit focus on West Africa; (B)—number of studies addressing conservation aspects of desiccation-tolerant plants in West Africa based on the 3 questions raised.

## 6.2. Exposure of desiccation-tolerant plants to anthropogenic pressures and the mitigating role of protected areas on West African inselbergs

The following 10 species have been selected as model: *Asplenium stuhlmannii* (Aspleniaceae), *Phymathosorus scolopendria* (Polypodiaceae), *Pellaea doniana* (Pteridaceae), *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae), *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minima* and *Sporobolus festivus* (Poaceae) and *Craterostigma yaundense* (Linderniaceae). The results show that while *A. stuhlmannii*, *P. doniana*, *S. festivus* and *A. pilosa* have a broad-ranging distribution, *P. scolopendria*, *O. aristatum*, *M. squamosa* and *C. yaundense* were registered on fewer inselbergs (Figure 24 and Table A5 in the Appendix 2). Also, the findings revealed that while a significant difference between the unprotected and protected areas was registered in relation to the species' exposure to quarrying, the species' exposure to climate change was similar across the protected and unprotected inselbergs in all future scenarios (Appendix 2; Table IV). However, the results show marked patterns among species protection and exposure to quarrying and climate change. Firstly, it is important to highlight that *C. yaundense* and *M. squamosa* were not present within the protected areas (Figures 25 and 27). Regarding the species' exposure to quarrying (Figures 26 and 28), all the species had at least one plant on an inselberg in which quarrying was registered (Figure 27; Appendix 2; Table A6). While *T. minima* had the lowest relative level of exposure to quarrying (7% of inselbergs, i.e., five out of seventy-one), *C. yaundense* showed the highest relative level of exposure to quarrying (60% of inselbergs, i.e., three out of five). The exposure of all the species to quarrying was reduced in absolute and relative values when inselbergs were included in the protected areas. While *T. minima* had the lowest relative reduction in exposure to quarrying in protected areas (1.1 times less exposed to quarrying), *O. aristatum* and *P. scolopendria* had their exposure to quarrying reduced from 18% and 17%, respectively, to 0% (Appendix 2; Table A7).

The species' exposure to climate change shows that all the species were more exposed to climate change in the most pessimistic scenario (SSP5) when compared to the most optimistic scenario (SSP1), especially in the farthest future (i.e., time-series 2071–2100; Figure 29, Appendix 2; Table A8). *M. indica* was the species with least exposure to climate change, although its exposure scores increased 2.5-fold over time in the most optimistic scenario (i.e., increasing from 0.06 to 0.15 in the 2011–2040 and 2070–2100 time-series, respectively) and 18.3-fold in the most pessimistic scenario (i.e., increasing from 0.06 to 1.1 in the 2011–2040 and 2070–2100 time-series, respectively). On the other hand, *C. yaundense* was the species most exposed to climate change, reaching an exposure score 25.6 times higher than that of *M. indica* in the most pessimistic scenario of the farthest future. Species such *C. yaundense* and *M. squamosus* (Figure 30) are more at risk with *C. yaundense* showing greater rises in its exposure to climate change over time, increasing 3.2-fold in the most optimistic scenario (i.e., increasing from 1.2 to 3.86 in 2011–2040 and 2071–2100, respectively) and 19.7-fold in the most pessimistic scenario (i.e., increasing from 1.48 in 2011–2040 to 28.18 in 2071–2100).

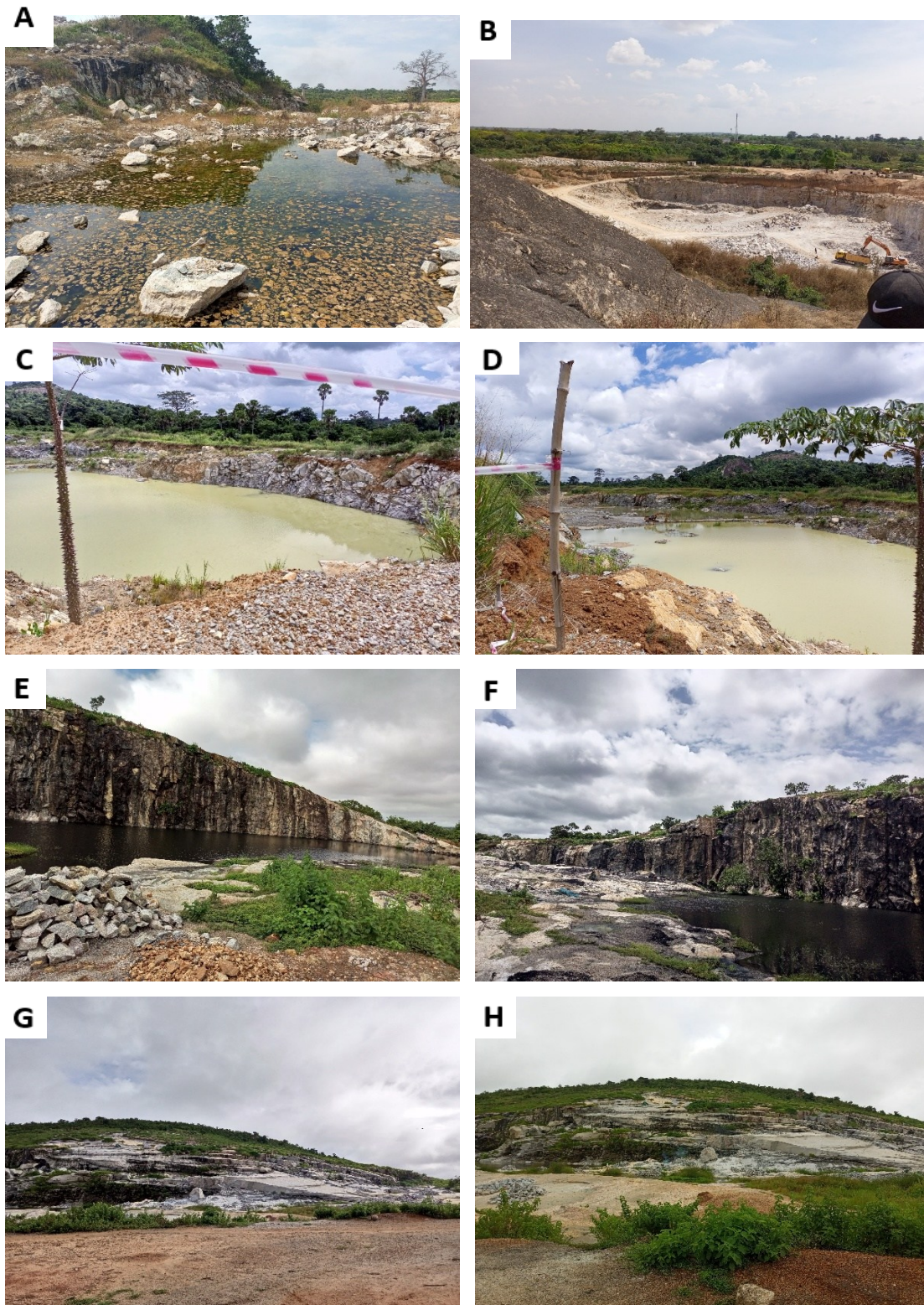


**Figure 24.** Uneven geographical distribution of 10 desiccation-tolerant vascular species across 123 inselbergs in West Africa.



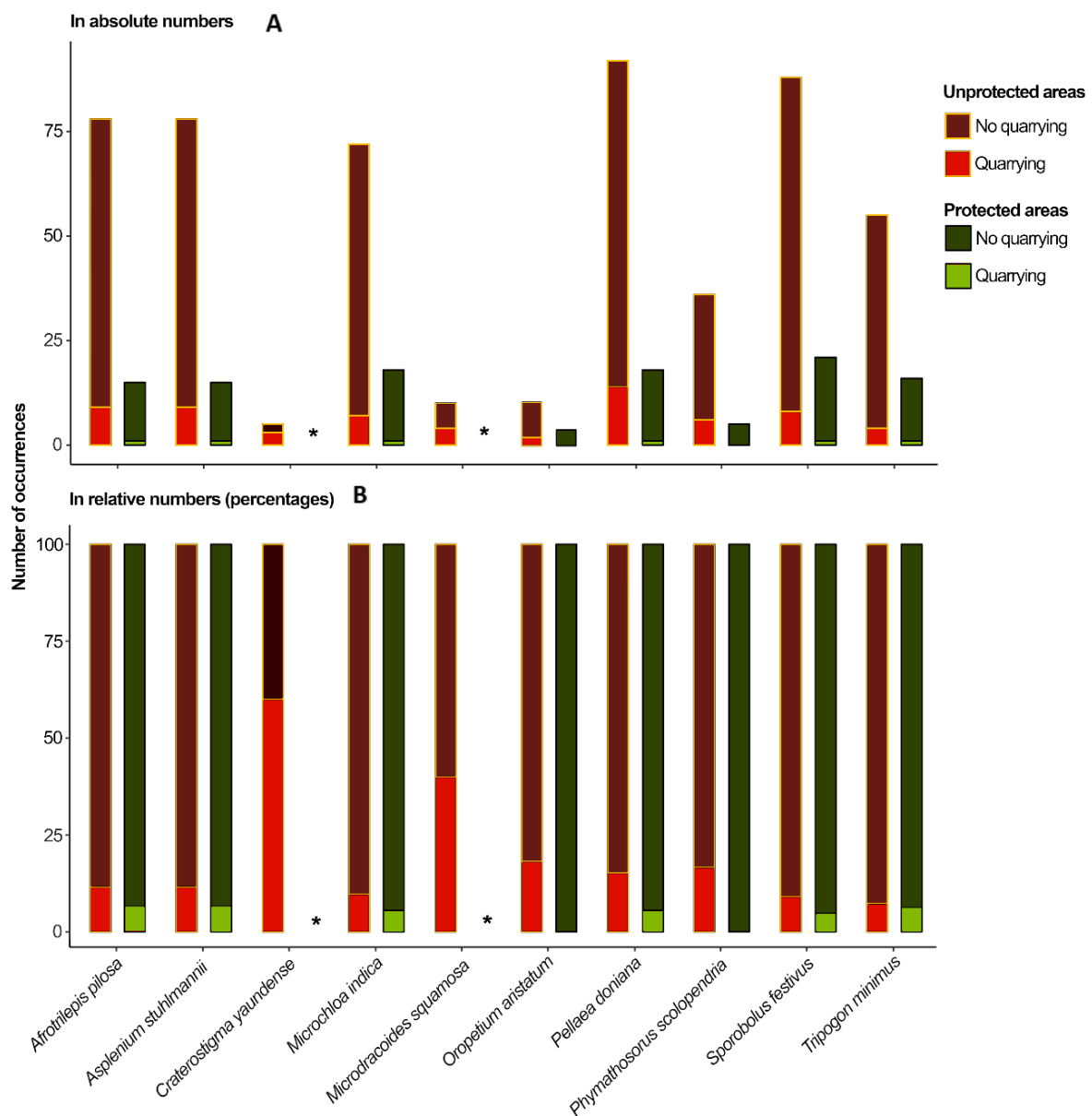
**Figure 25.** Species that most require conservation attention and suffer from anthropogenic threats are ones least favored by current protection areas. (A)-*Microdracoides squamosa* (Cyperaceae); (B)-*Craterostigma yaundense* (Linderniaceae).





**Figure 26.** Quarrying activities causing the removal of desiccation-tolerant vascular plants in Côte d'Ivoire. Modern (mechanized) quarrying: (A-B) Bouaké (November 2022); (C-D) Lolobo (July 2023). Traditional (artisanal) quarrying: (E-F) Northeastern Korhogo (August 2023); (G-H) Central Korhogo (August, 2023).

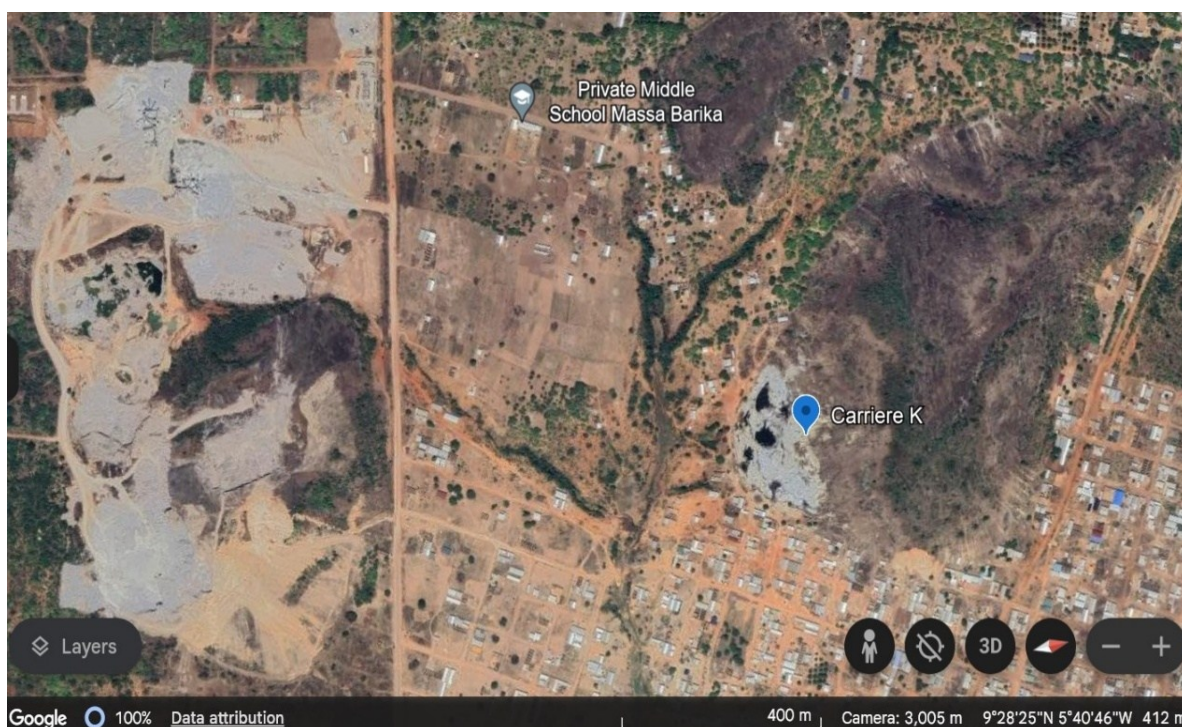




**Figure 27.** Impact of quarrying on the habitats of the 10 evaluated plant species.

**A:** Absolute numbers reflecting the total number of occurrence records in quarried and non-quarried areas within protected and unprotected sites. **B:** Relative numbers (percentages) indicating the proportion of each species' known occurrences affected by quarrying, allowing comparison among species with different data availability.

This figure illustrates the extent of exposure to quarrying for each species in unprotected and protected areas in both absolute and relative numbers. \*—no presence of the species was registered in such areas.

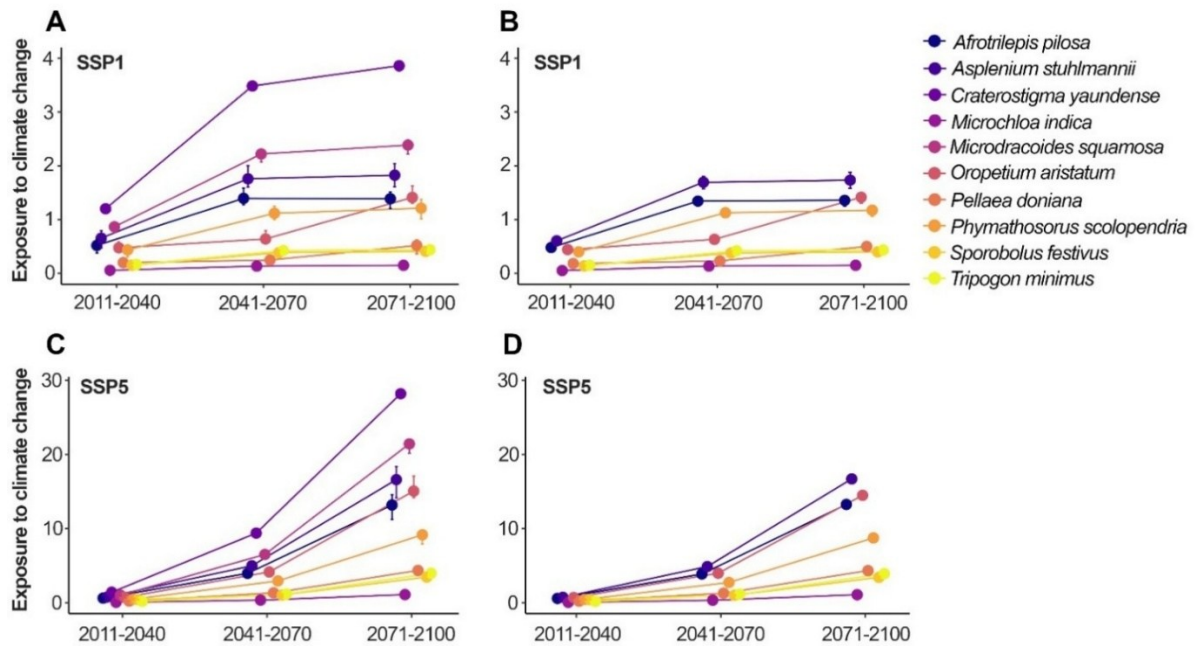


**Figure 28.** Impact of quarrying on inselbergs: Case of mining in a protected area based in the Korhogo region (Côte d'Ivoire).

**Table IV.** Comparison between unprotected and protected areas concerning species exposure to quarrying and climate change

| Anthropogenic drivers | Scenario/Period  | Unprotected Mean $\pm$ SD | Protected Mean $\pm$ SD | W-Value/t-Value | <i>p</i> -Value |
|-----------------------|------------------|---------------------------|-------------------------|-----------------|-----------------|
| Quarrying             | -                | 0.80 $\pm$ 0.17           | 0.20 $\pm$ 0.15         | W= 80           | 0.0004          |
| Climate change        | SSP1 (2011–2040) | 0.46 $\pm$ 0.35           | 0.29 $\pm$ 0.19         | t= 1.17         | 0.7809          |
|                       | SSP1 (2041–2070) | 1.46 $\pm$ 0.97           | 0.85 $\pm$ 0.56         | t= 1.04         | 0.9456          |
|                       | SSP1 (2071–2100) | 1.75 $\pm$ 1.15           | 0.95 $\pm$ 0.56         | t= 1.05         | 0.9297          |
|                       | SSP5 (2011–2040) | 0.68 $\pm$ 0.39           | 0.53 $\pm$ 0.22         | t= 1.1          | 0.8592          |
|                       | SSP5 (2041–2070) | 3.57 $\pm$ 2.81           | 2.90 $\pm$ 1.76         | t= 1.03         | 0.9519          |
|                       | SSP5 (2071–2100) | 11.64 $\pm$ 8.23          | 8.47 $\pm$ 5.57         | t= 0.93         | 1               |

Mann–Whitney U test was used for quarrying exposure, and t-test for climate change exposure. Climate change *p*-values were adjusted using Bonferroni correction.



**Figure 29.** Projected climate change exposure of 10 desiccation-tolerant species in West Africa under Low (SSP1) and High (SSP5) Emission Scenarios (2011–2100) within protected and unprotected areas. **A.)** Exposure to climate change under SSP1 within Unprotected areas. **A.)** Exposure to climate change under SSP1 within Unprotected areas. **B.)** Exposure to climate change under SSP1 within Protected areas. **C.)** Exposure to climate change under SSP5 within Unprotected areas. **D.)** Exposure to climate change under SSP5 within Protected areas.

This figure illustrates the projected mean exposure of 10 desiccation-tolerant plant species to climate change under two different climate scenarios within protected and unprotected areas: SSP1, representing a low-emission, sustainable pathway; and SSP5, a high-emission, fossil-fuel-intensive pathway. Projections are shown across time series: 2011–2040, 2041–2070, and 2071–2100.





**Figure 30.** Possible effects of climate change on the desiccation tolerance ability of desiccation-tolerant vascular plants.

Red arrows point to branches of *M. squamosa* that shrank, indicating that they did not tolerate desiccation and rehydration cycles.

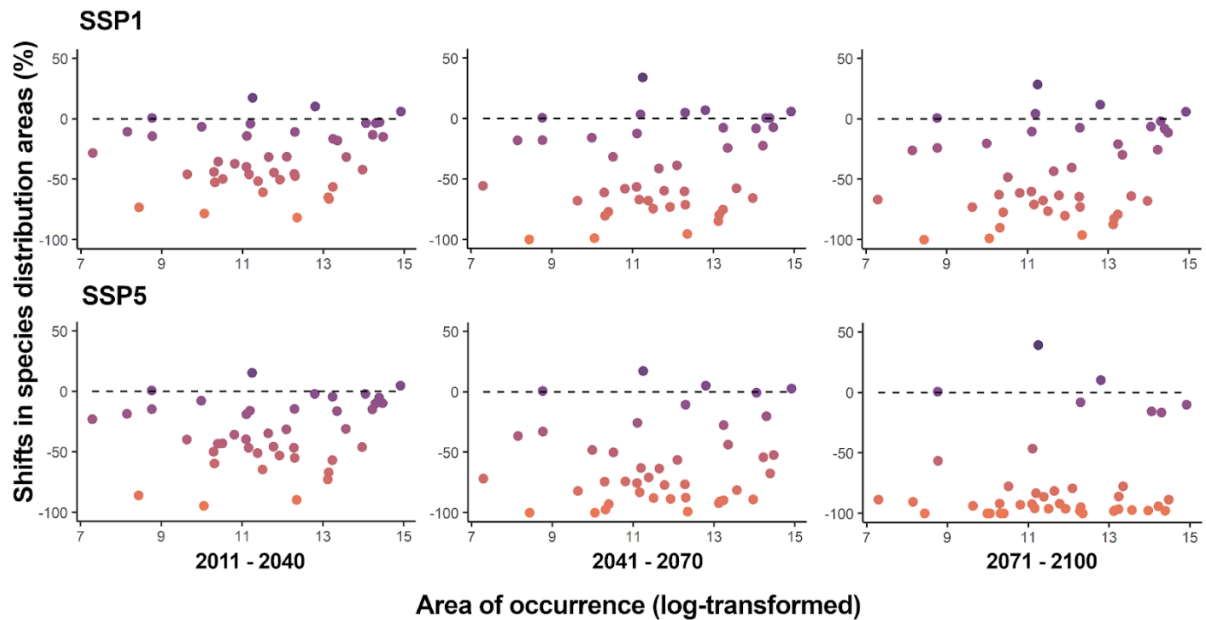
## Chapter 7: Impacts of climate change on desiccation-tolerant plant distribution and diversity

### 7.1. Distribution of desiccation-tolerant vascular plants and impact of climate change

The modelling results, which assess the impact of climate change on species distribution, indicate that most of the DT plants modelled in West Africa will be negatively impacted by climate change in both the most optimistic (i.e., SSP1) and pessimistic scenarios (SSP5; Figure 31). For most species, projected distribution areas (geographical range) decline progressively through time, with losses generally more pronounced under SSP5 and during the late-century period (2071-2100). Certain species, such as *Cheilanthes inaequalis* (Kunze) Mett., *Microchloa kunthii* Desv. and *Craterostigma yaundense* (S.Moore) Eb.Fisch., Schäferh. & Kai Müll. exhibit particularly strong contractions across all future scenarios (Figure 32, Table A12, Appendix 3). A loss of 100% of current distribution areas was registered for the species *C. inaequalis* and *C. yaundense* in 4 and 2 (out of 6) future scenarios, respectively. *C. inaequalis*, which currently occupies  $4615 \times 10^3 \text{ km}^2$ , is projected to lose its entire distribution under both scenarios by mid- to late-century, with 100% loss recorded in 4 out of 6 future projections. Similarly, *C. yaundense* declines from  $23.2 \times 10^3 \text{ km}^2$  to near-zero values under SSP1 by 2041-2070, and is projected to lose 100% of its distribution under SSP5 from 2041-2070 onward. *M. kunthii* also shows severe reductions, declining from  $231.2 \times 10^3 \text{ km}^2$  to  $9.0 \times 10^3 \text{ km}^2$  (−96%) under SSP1 and to  $0.1 \times 10^3 \text{ km}^2$  (−100%) under SSP5 by 2071-2100.

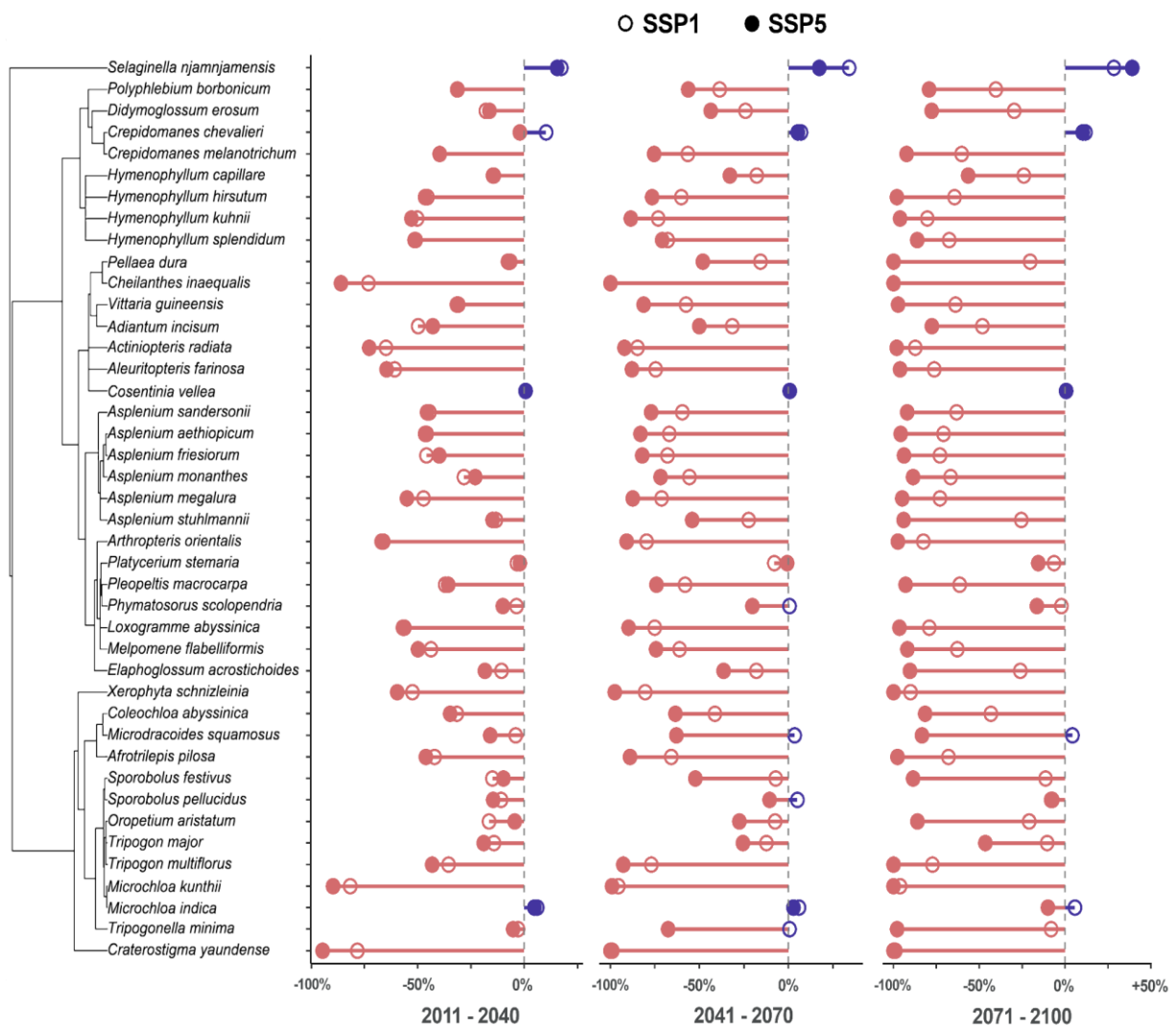
In contrast to the general pattern of decline observed, species that would experience a positive impact of climate change were few and not restricted to specific taxonomic groups. *Selaginella njamnjamensis* Hieron. was the species most positively affected by climate change in all future scenarios, it shows consistent increases under both scenarios, expanding from  $76.7 \times 10^3 \text{ km}^2$  at present to  $98.4 \times 10^3 \text{ km}^2$  (+28%) under SSP1 and  $106.7 \times 10^3 \text{ km}^2$  (+39%) under SSP5 by 2071-2100. Followed by *Crepidomanes chevalieri* (Christ) Ebihara & Dubuisson, which increases from  $360.9 \times 10^3 \text{ km}^2$  to  $403.4 \times 10^3 \text{ km}^2$  (+12%) under SSP1 and  $397.9 \times 10^3 \text{ km}^2$  (+10%) under SSP5 and *Microchloa indica* (L. f.) P. Beauv., which expands by 3-6% under SSP1 and remains broadly stable under SSP5 until the late century Table A12, Appendix 3).

Overall, complete loss of distribution (geographical ranges) is projected for only one species (≈2%) under SSP1, compared to five species (≈12%) under SSP5, while positive distributional responses are restricted to four species (≈10%) across all projections (Figures A6-47; Appendix 3).



**Figure 31.** Shifts in species distribution areas (in percent) by species area of occurrence (log-transformed) in three different time series (2011-2040, 2041-2070, 2071-2100) of two different future scenarios (SSP1, the most sustainable pathway, and SSP5, the most sustainable pathway, and SSP5, the most fossil-fuel-intensive pathway).

The dashed line represents the threshold where shifts in species distribution areas are either negative or positive, in case of contraction or expansion (colour gradient from red for contraction to blue for expansion) of areas owing to climate change, respectively.



**Figure 32.** Projected changes in distribution areas of desiccation-tolerant vascular plants in West Africa under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

Red color = Contraction/Loss in the distribution range areas.

Blue color = Expansion/Gain in the distribution range areas.

A value of 0% indicates no change in distribution range areas, while negative and positive values represent the percentage of contraction and expansion in species distribution areas due to climate change, respectively.

## **7.2. Diversity patterns of desiccation-tolerant vascular plants and impact of climate change.**

### **7.2.1. Centers of diversity**

Regarding the centers of diversity for DT plants, locations were classified based on species as follows: very low diversity (species richness ranging from 1 to 2 species), low diversity (species richness ranging from 3 to 5 species), moderated diversity (species richness ranging from 6 to 11 species), high diversity (species richness ranging from 12 to 26 species), and very high diversity (species richness ranging from 27 to 28 species).

Centers of diversity for DT plants (i.e., locations exhibiting a high and very high species richness) are identified in areas such : (1) in the Guinea highlands, which also includes montane locations in Sierra Leone, Liberia and Côte d'Ivoire; (2) in the Togo Mountains; (3) along the Cameroon volcanic line, which also includes the islands Bioko and Sao Tomé et Príncipe; (4) a region extending from central Cameroon to most parts of continental Equatorial Guinea; besides (5) small enclaves of high species richness along the coastline of South-South of Nigeria and Cameroon (Figure 33). Those regions identified as centers of diversity are often mountainous or topographically complex, offering microclimatic heterogeneity, edaphic diversity and climatic refugia, which may promote both speciation and species persistence.

### **7.2.2. Centers of endemism**

For the centers of endemism for DT plants, locations were classified as of very low endemism (endemism richness ranging from 0.0000010 to 0.6931481; please see the Methods section for more information about how values of endemism richness were calculated), low endemism (endemism richness ranging from 0.6931482 to 2.0794424), moderated endemism (endemism richness ranging from 2.0794425 to 3.4657368), high endemism (endemism richness ranging from 3.4657369 to 7.4217767) and very high endemism (endemism richness ranging from 7.4217768 to 9.9111592).

As centers of endemism for DT plants (i.e., locations exhibiting a high and very high endemism richness) the following areas were identified: (1) in Cabo Verde islands; (2) in Guinea highlands, including montane locations in Sierra Leone, Southern Liberia and Western Côte d'Ivoire; (3) in Southern Ghana (Volta region) and Togo Mountains; (4) in Kaduna State in north-west region of Nigeria, (5) Aïr Massif in Northern Niger; (6) along the Cameroon volcanic line, which also includes the islands Bioko and Sao Tomé et Príncipe; (7) in the region extending from Southern Cameroon to continental parts of Equatorial Guinea; besides (8) enclaves of high endemism richness along the West African coastline, from Senegal to Cameroon, which include subregions



(i), (ii) and (iii) that together constitute the eighth center of endemism (Figure 34). Same as the centers of diversity, the identified centers of endemism are also mountainous or topographically complex, offering microclimatic heterogeneity, edaphic diversity and climatic refugia.

### **7.2.3. Conservation priority areas for DT plants**

The modeling reveals areas that not only harbor a high number of DT species but also exhibit notable levels of endemism. These areas were underscored as the priority areas for the conservation of DT plants and are: the Guinea Highlands, the Togo Mountains, the Cameroon Volcanic Line (including Bioko, São Tomé and Príncipe Islands) and the region spanning from central Cameroon to continental Equatorial Guinea. The results also show that only 11% of those priority areas for the conservation of DT plants currently fall within protected areas (Figure 35, Current distribution). The Guinea Highlands are projected to support much lower richness even under the most optimistic scenarios (by 2071-2100). In contrast, the continental parts of the Cameroon Volcanic Line are projected to serve as important climate refugia, for both high species richness and endemism, even under pessimistic scenarios (by 2071-2100).

### **7.2.4. Projected changes in species richness and endemism under future climate scenarios**

Projections of the impact of climate change on species richness show that the current centers of diversity for DT plants are going to contract under future climate change (Figure 36), with the extent of this contraction becoming more severe under the pessimistic scenario (SSP5) compared to the optimistic scenario (SSP1; Table V). This contraction becomes particularly pronounced during the late-century period (2071-2100), where no location will show a very high species richness of DT plants, and only disjunct patches along the Cameroon volcanic line are predicted to maintain a high species richness of DT plants.

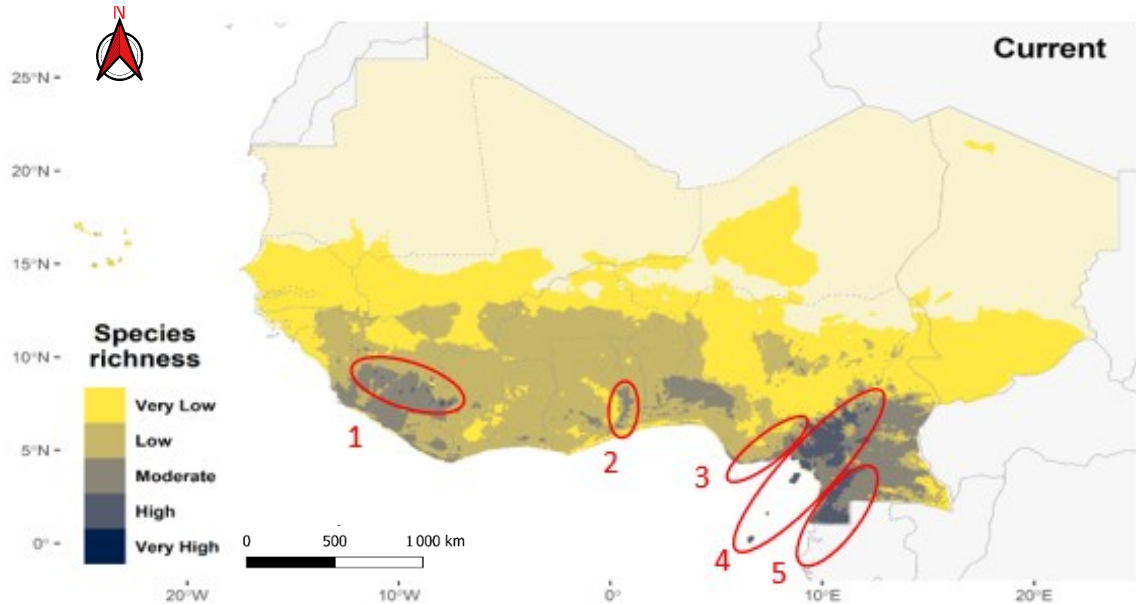
To be more precise, the results show that for example, areas of high species richness currently cover  $103.4 \times 10^3 \text{ km}^2$ . Under SSP1, these areas decline to  $73.2 \times 10^3 \text{ km}^2$  (–29%) in 2011–2040,  $51.5 \times 10^3 \text{ km}^2$  (–50%) in 2041–2070, and  $46.9 \times 10^3 \text{ km}^2$  (–55%) in 2071–2100. Under SSP5, the contraction is more severe, the decline is stronger, with high-richness areas decreasing to  $66.1 \times 10^3 \text{ km}^2$  (–36%),  $26.7 \times 10^3 \text{ km}^2$  (–74%), and  $10.6 \times 10^3 \text{ km}^2$  (–90%), respectively (Table A13, Appendix 3). Areas of very high species richness, currently limited to  $0.02 \times 10^3 \text{ km}^2$ , persist only until 2011–2040 under SSP1 ( $0.02 \times 10^3 \text{ km}^2$ , +25%) and are absent thereafter. Under SSP5, very high richness areas are absent from 2011–2040 onward (Table A13, Appendix 3). In contrast, areas classified as very low species richness currently cover  $2493.6 \times 10^3 \text{ km}^2$  and are projected to expand under both scenarios.

Under SSP1, these areas increase to  $3004.0 \times 10^3 \text{ km}^2$  (+20%) by 2011–2040,  $3076.1 \times 10^3 \text{ km}^2$  (+23%) by 2041–2070, and  $3175.8 \times 10^3 \text{ km}^2$  (+27%) by 2071–2100. Under SSP5, very low richness areas expand to  $3016.1 \times 10^3 \text{ km}^2$  (+21%),  $4100.0 \times 10^3 \text{ km}^2$  (+64%), and  $4060.8 \times 10^3 \text{ km}^2$  (+63%), respectively (Table A13, Appendix 3).

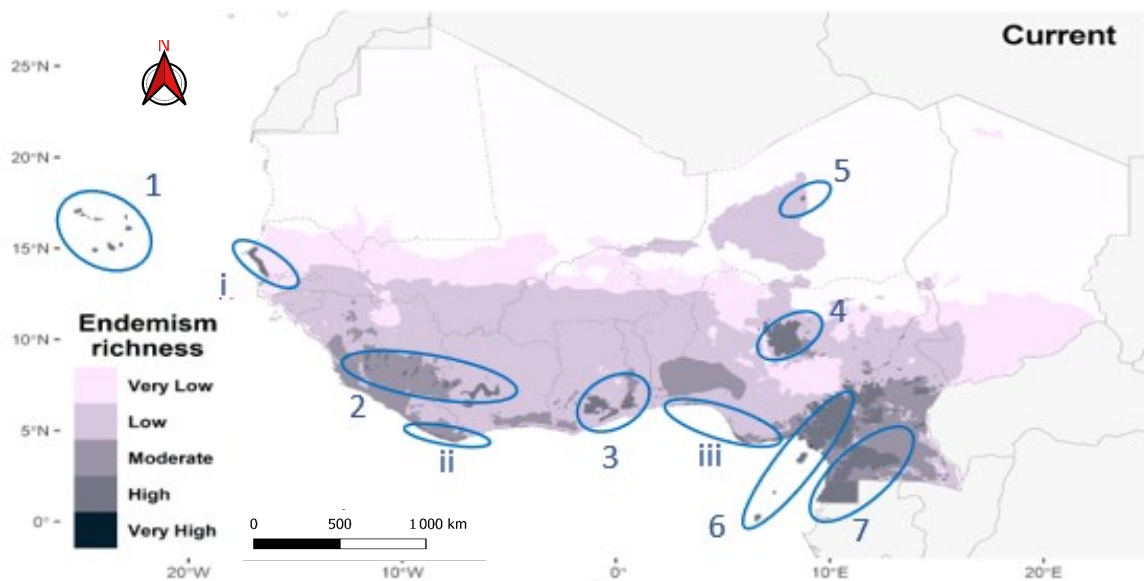
Projections show that the current centers of endemism are also likely to shrink under future climate scenarios (Figure 37), with the degree of reduction more marked under SSP5 than SSP1 (Table V). However, climate change will not promote an opposite shift in areas of high and very high endemism richness of DT plants. While areas of high endemism richness will be reduced, areas of very high endemism richness will increase in size.

For example, areas of high endemism richness currently cover  $331.7 \times 10^3 \text{ km}^2$ . Under SSP1, these areas contract to  $265.3 \times 10^3 \text{ km}^2$  (–20%) by 2011–2040,  $214.6 \times 10^3 \text{ km}^2$  (–35%) by 2041–2070, and  $198.0 \times 10^3 \text{ km}^2$  (–40%) by 2071–2100. Under SSP5, areas decrease to  $245.2 \times 10^3 \text{ km}^2$  (–26%),  $172.6 \times 10^3 \text{ km}^2$  (–48%), and  $128.4 \times 10^3 \text{ km}^2$  (–61%), respectively (Table A13; Appendix 3). Also, areas of very high endemism richness, currently restricted to  $0.1 \times 10^3 \text{ km}^2$ , expand under both scenarios. Under SSP1, these areas increase to  $0.8 \times 10^3 \text{ km}^2$  (+628%) in 2011–2040,  $0.9 \times 10^3 \text{ km}^2$  (+694%) in 2041–2070, and  $0.9 \times 10^3 \text{ km}^2$  (+710%) in 2071–2100.

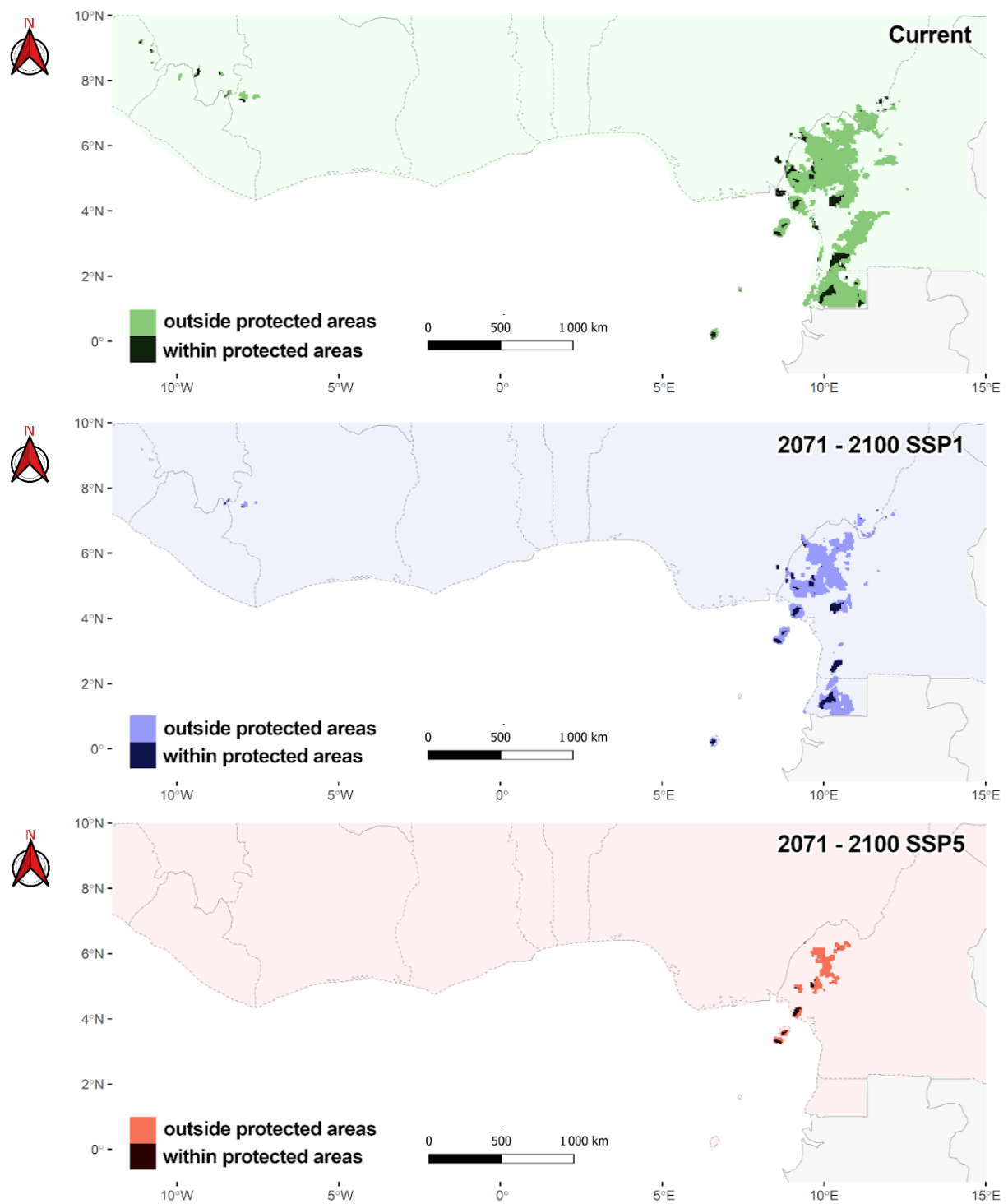
Under SSP5, they increase to  $1.6 \times 10^3 \text{ km}^2$  (+1313%),  $1.5 \times 10^3 \text{ km}^2$  (+1251%), and  $4.3 \times 10^3 \text{ km}^2$  (+3765%; Table A13; Appendix 3) across the three future periods respectively. While areas of very low endemism richness currently cover  $1407.7 \times 10^3 \text{ km}^2$ . Under SSP1, these areas slightly increase to  $1960.2 \times 10^3 \text{ km}^2$  (+39%) by 2011–2040,  $1961.9 \times 10^3 \text{ km}^2$  (+39%) by 2041–2070, and  $2026.1 \times 10^3 \text{ km}^2$  (+44%) by 2071–2100. Under SSP5, very low endemism areas expand to  $1798.2 \times 10^3 \text{ km}^2$  (+28%),  $2159.6 \times 10^3 \text{ km}^2$  (+53%), and  $3082.1 \times 10^3 \text{ km}^2$  (+119%) across the three future periods, respectively (Table A13; Appendix 3). Very low endemism richness in both scenarios will slightly increase.



**Figure 33.** Center of diversity of desiccation-tolerant vascular plants in West Africa according to the species richness (from a taxonomic perspective). (1) in the Guinea highlands; (2) Togo Mountains; (3) Cameroon volcanic line; (4) Cameroon to most parts of continental Equatorial Guinea; (5) Coastline of South-South of Nigeria and Cameroon



**Figure 34.** Center of endemism of desiccation-tolerant vascular plants in West Africa according to the endemism richness (from an endemism perspective). (1) in Cabo Verde; (2) Guinea highlands; (3) Southern Ghana (Volta region) and Togo Mountains; (4) Kaduna State (Nigeria) ; (5) Air Massif (Niger); (6) Cameroon volcanic line; (7) Southern Cameroon to continental Equatorial Guinea; (8) Coastline, from Senegal to Cameroon, which include subregions (i), (ii) and (iii) that together constitute the eighth center of endemism.

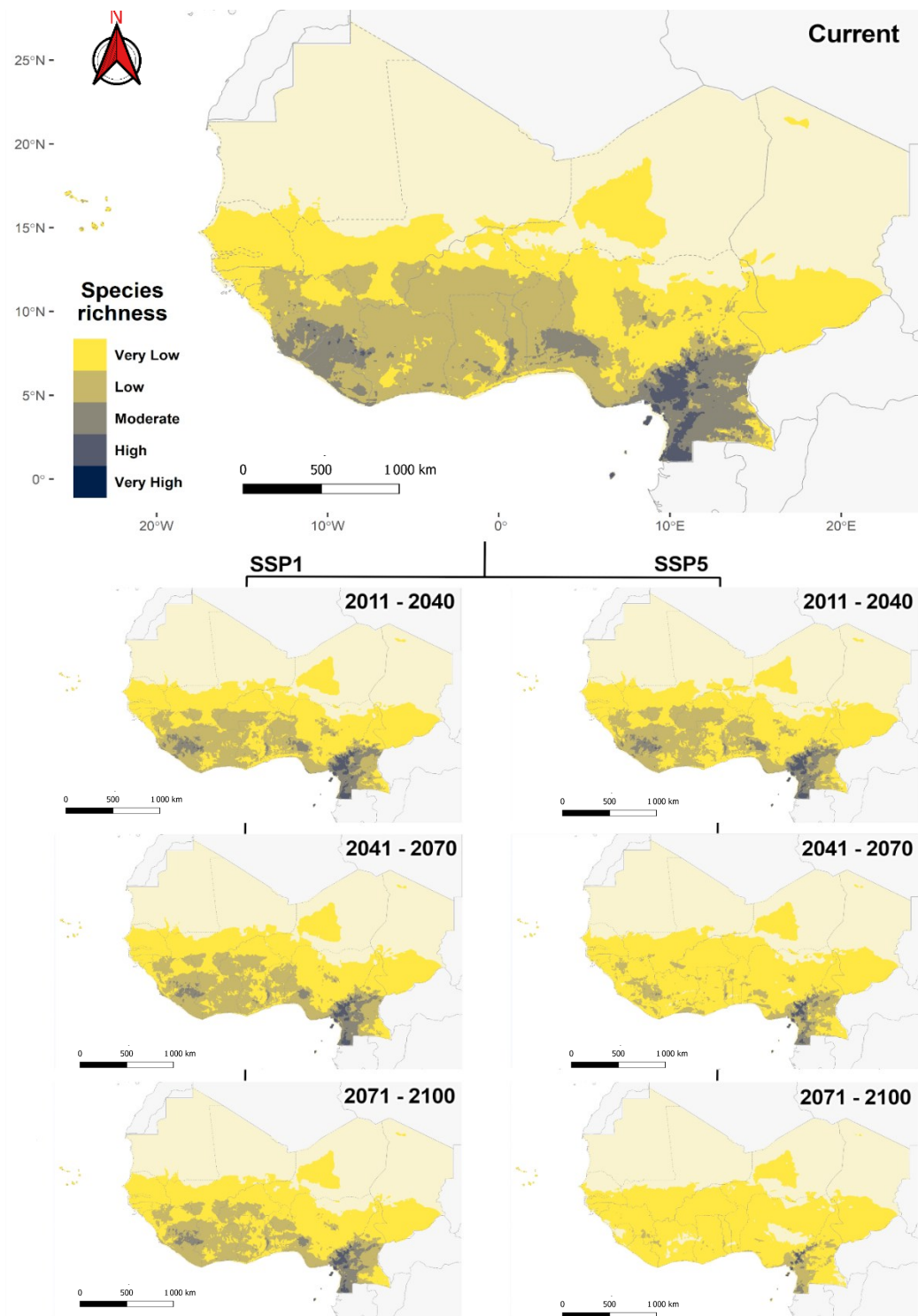


**Figure 35.** Priority areas for the conservation of desiccation-tolerant vascular plants outside and within protected areas from West Africa in the present and in the farthest future times-series (2071-2100).

**Table V.** Area shifts of diversity patterns (from a taxonomic and endemism perspective) of desiccation-tolerant vascular plants in West Africa owing to climate change.

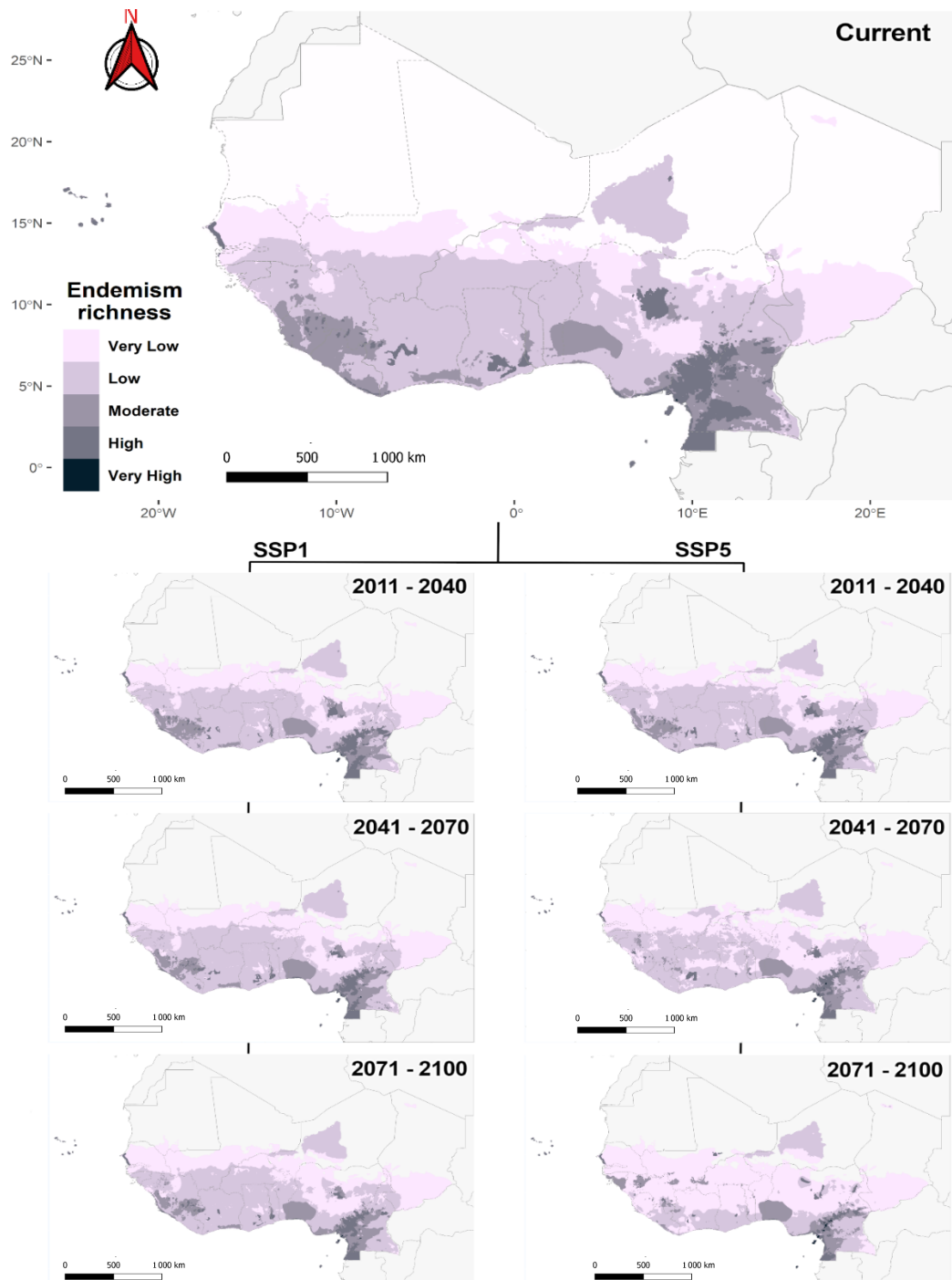
|                   | SSP1      |           |           | SSP5      |           |           |
|-------------------|-----------|-----------|-----------|-----------|-----------|-----------|
|                   | 2011-2040 | 2041-2070 | 2071-2100 | 2011-2040 | 2041-2070 | 2071-2100 |
| Species richness  |           |           |           |           |           |           |
| Very low          | +20 %     | +23 %     | +27 %     | +21 %     | +64 %     | +63 %     |
| Low               | -10 %     | -10 %     | -17 %     | -11 %     | -63 %     | -86 %     |
| Moderate          | -43 %     | -56 %     | -59 %     | -49 %     | -83 %     | -95 %     |
| High              | -29 %     | -50 %     | -55 %     | -36 %     | -74 %     | -90 %     |
| Very High         | +25 %     | -100 %    | -100 %    | -100 %    | -100 %    | -100 %    |
| Endemism richness |           |           |           |           |           |           |
| Very low          | +39 %     | +39 %     | +44 %     | +28 %     | +53 %     | +119 %    |
| Low               | -8 %      | -4 %      | -6 %      | -2 %      | -5 %      | -48 %     |
| Moderate          | -19 %     | -21 %     | -26 %     | -22 %     | -48 %     | -42 %     |
| High              | -20 %     | -35 %     | -40 %     | -26 %     | -48 %     | -61 %     |
| Very High         | +628 %    | +694 %    | +710 %    | +1313 %   | +1251 %   | +3765 %   |

The impact of climate change was evaluated using different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100). Negative values describe the contraction of areas of a given class of species and endemism richness, while positive values describe the expansion of areas of a given class of diversity and endemism richness.



**Figure 36.** Impact of climate change on the species richness (Current species richness center) of desiccation-tolerant vascular plants in West Africa under SSP1 and SSP5.

The impact of climate change was evaluated considering different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100). Regions with high and very high species richness were considered the centers of diversity for DT plants.



**Figure 37.** Impact of climate change on the endemism richness (Current endemism richness center) of desiccation-tolerant vascular plants in West Africa under SSP1 and SSP5.

The impact of climate change was evaluated considering different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100). Regions with high and very high endemism richness were considered the centers of endemism for DT plants.

## Chapter 8: Influence of soil on intraspecific variation in ecological strategies of desiccation-tolerant plants in Côte d'Ivoire

Across the seven localities in Côte d'Ivoire (Korhogo, Niangbo, Séguéla, Silakoro, Dabakala, Bouaké and Kokumbo), 17 inselbergs within 11 sites were sampled. Altogether, the species were collected within 138 plots. Based on the soil presence in the plots, of the 18 inselbergs sampled, 10 were retained. *Afrotrilepis pilosa* has been collected within 18 plots across 8 inselbergs, *Microchloa indica* was collected from 20 plots on 5 inselbergs; *Sporobolus festinus* has been collected within 24 plots across 6 inselbergs; *Tripogonella minima* has been collected within 21 plots across 7 inselbergs.

### 8.1. Composition of C-S-R-selection strategies by species

The CSR classification of the four studied grass species shows clear differences in ecological strategies, ranging from highly specialized stress-tolerant to more flexible, mixed-strategy types (Figure 38). Among these, stress-tolerance (S-selection) emerged as the dominant strategy across most individuals. *Afrotrilepis pilosa* displayed a more mixed strategy profile, with 55.55% of individuals classified as CSR, 33.33% as C/CSR and 11.11% as S/CSR (mean CSR = 38:32:30), as shown in Figure 40 and Table VI. *Microchloa indica* showed a strong skew toward S-selection, with 95% of individuals classified as S and an additional 5% as S/CSR (mean CSR = 1.6:96.6:1.8; Table VII). *Sporobolus festinus*, had 91.66% of individuals categorized as S, 4.16% as S/CS and 4.16% as S/SR, (mean CSR = 6:91:3; Table VIII). In contrast, *Tripogonella minima* was the most specialized species, with 100% of individuals exhibiting a pure stress-tolerant (S) strategy (mean CSR = 1:99:0; Table IX).

### 8.2. Relationship between CSR strategies and leaf traits

For *Afrotrilepis pilosa*, the LA was highly variable, ranging from 1,405.5 mm<sup>2</sup> to 545,820.5 mm<sup>2</sup>, with the largest values linked to individuals expressing C/CSR strategies. The LDMC averaged around 31.6-54.4%, which is particularly high for individuals expressing C/CSR strategies. The SLA shows variation ranging from 33.4 to 433.8 mm<sup>2</sup> mg<sup>-1</sup>, with higher SLA linked to individuals showing C/CSR strategies (Table VI).

For *Microchloa indica*, the LA was very small, ranging from 3.38 to 218.36 mm<sup>2</sup>, consistent with the S strategy dominance, with the smallest value more linked to S individuals and the highest for S/SR. For the LDMC, the values are within 26.32 (S)-71.64% (S/SR). The SLA, shows values ranging within 1.17-23.06 mm<sup>2</sup> mg<sup>-1</sup>, being slightly elevated for S/SR individual (Table VII).



For *Sporobolus festivus* the LA ranged within 40.7-361.2 mm<sup>2</sup>, with the largest LA values in individuals showing S/CS strategies. The LDMC varies within 31.9-56.7%. The SLA ranged from 3.8 to 14.7 mm<sup>2</sup> mg<sup>-1</sup> (Table VIII).

For *Tripogonella minima* the LA ranges within 3.5-69.7 mm<sup>2</sup>. The LDMC ranged within 46.2-75.3%. The SLA ranges within 1.9-9.4 mm<sup>2</sup> mg<sup>-1</sup>, consistent with low growth rates and resource conservation, both indicative of stress-adapted leaf economics (Table IX).

### 8.3. Relationship between CSR strategies and soil variables

The correlation analysis (Figure 20) revealed strong associations among certain soil variables. Organic matter (OM) was perfectly correlated with organic carbon (CO;  $r = 1$ ) and showed strong correlations with total nitrogen (N;  $r = 0.7$ ) and cation exchange capacity (CEC;  $r = 0.9$ ). Potassium (K) was also strongly correlated with CEC ( $r = 0.74$ ) and with OM ( $r = 0.59$ ). Conversely, pH ( $r \leq 0.34$  with all other retained variables), clay content ( $r \leq 0.39$ ), soil moisture ( $r \leq 0.31$ ) and available phosphorus ( $r \leq 0.34$ ) displayed low correlations with each other, indicating they represent distinct environmental gradients. Based on these results, pH, clay content, soil moisture, organic matter and phosphorus were selected for subsequent multivariate analyses. Clay and moisture were interpreted as indicators of stress-related environmental constraints (water availability, soil structure), whereas pH, OM and P were considered proxies for competition-related nutrient and resource availability. Statistical testing revealed no significant relationships between CSR strategy components and the selected soil variables across the four species.

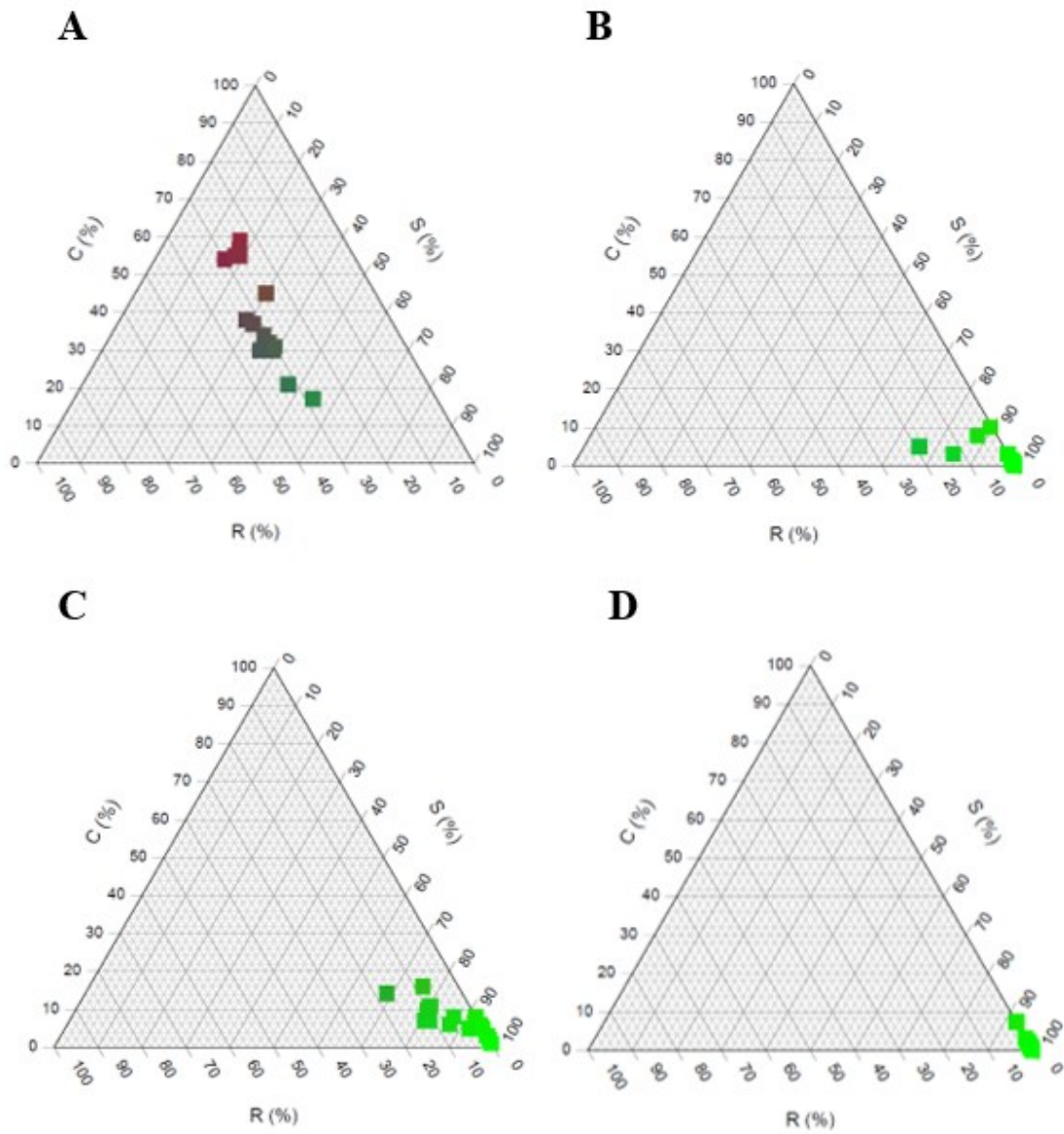
For *Afrotrilepis pilosa*, competitiveness was unaffected by OM, P and pH ( $p$ -values = 0.94, 0.77, 0.46; Figure 39) and stress tolerance also showed no association with clay and moisture ( $p$ -values = 0.73, 0.98, Figure 40).

For *Microchloa indica*, competitiveness was found to be unaffected by OM, P and pH ( $p$ -values = 0.12, 0.09, 0.74, Figure 41). Stress-tolerance was also found to be unrelated to Clay ( $p$ -values = 0.06) and Moisture ( $p = 0.61$ , Figure 42).

For *Sporobolus festivus*, competitiveness was not significantly influenced by OM, P, or pH ( $p$ -values = 0.66, 0.98, 0.26, Figure 43), nor was stress-tolerance by clay or moisture ( $p$ -values = 0.53, 0.42, Figure 44).

For *Tripogonella minima*,  $p$ -values for the effects of OM, P and pH on the competitiveness were, respectively, 0.21, 0.08 and 0.95, (Figure 45). For the effect of Clay and Moisture on the stress-tolerance of *Tripogonella minima*,  $p$ -values were 0.38 and 0.65, respectively (Figure 46).

The  $p$ -values show that all the soil variables measured have a non-significant effect on the species' ecological strategies.



**Figure 38.** Relative proportion (%) of C, S and R selection for: **A.** *Afrotrilepis pilosa* CSR = 38:32:30. **B.** *Microchloa indica*, CSR = 1.6:96.6:1.8. **C.** *Sporobolus festivus*, CSR = 6:91:3. **D.** *Tripogon minima*, CSR = 1:99:0.

The colour of each square derives from the conversion of the C, S, and R ratio (secondary CSR strategy classes suggested by Grime 2001) to red, green, and blue.

C-S-R selection with C= Competitors; S= Stress-tolerators; R= Ruderals

**Table VI.** CSR strategies, following Pierce *et al.* (2017), for *Afrotrilepis pilosa*.

| Species                    | C%   | S%   | R%   | Strategy class | LA (mm <sup>2</sup> ) | LDMC (%) | SLA (mm <sup>2</sup> mg-1) |
|----------------------------|------|------|------|----------------|-----------------------|----------|----------------------------|
| <i>Afrotrilepis pilosa</i> | 59.2 | 16.6 | 24.2 | C/CSR          | 242198.5              | 44.2     | 226.0                      |
| <i>Afrotrilepis pilosa</i> | 45.5 | 29.7 | 24.9 | C/CSR          | 14194.3               | 36.9     | 40.5                       |
| <i>Afrotrilepis pilosa</i> | 54.3 | 15.7 | 30.0 | C/CSR          | 69119.9               | 36.8     | 273.7                      |
| <i>Afrotrilepis pilosa</i> | 56.2 | 18.4 | 25.4 | C/CSR          | 35272.6               | 31.6     | 65.4                       |
| <i>Afrotrilepis pilosa</i> | 32.4 | 37.0 | 30.6 | CSR            | 9762.1                | 50.8     | 75.2                       |
| <i>Afrotrilepis pilosa</i> | 29.5 | 39.5 | 31.0 | CSR            | 5736.5                | 45.1     | 53.5                       |
| <i>Afrotrilepis pilosa</i> | 31.4 | 37.5 | 31.1 | CSR            | 5867.6                | 41.3     | 49.6                       |
| <i>Afrotrilepis pilosa</i> | 30.5 | 38.3 | 31.2 | CSR            | 6852.5                | 46.5     | 60.3                       |
| <i>Afrotrilepis pilosa</i> | 55.0 | 18.2 | 26.8 | C/CSR          | 545820.5              | 51.7     | 433.8                      |
| <i>Afrotrilepis pilosa</i> | 54.7 | 19.0 | 26.3 | C/CSR          | 525644.3              | 54.4     | 409.9                      |
| <i>Afrotrilepis pilosa</i> | 30.0 | 36.8 | 33.2 | CSR            | 4759.2                | 38.3     | 49.2                       |
| <i>Afrotrilepis pilosa</i> | 37.9 | 29.1 | 33.0 | CSR            | 8433.4                | 34.0     | 55.3                       |
| <i>Afrotrilepis pilosa</i> | 30.5 | 39.0 | 30.4 | CSR            | 4795.6                | 39.9     | 42.1                       |
| <i>Afrotrilepis pilosa</i> | 37.5 | 30.5 | 32.0 | CSR            | 10917.5               | 39.4     | 68.6                       |
| <i>Afrotrilepis pilosa</i> | 34.1 | 34.5 | 31.3 | CSR            | 11726.7               | 49.6     | 86.7                       |
| <i>Afrotrilepis pilosa</i> | 17.1 | 54.4 | 28.5 | S/CSR          | 1405.5                | 49.1     | 33.4                       |
| <i>Afrotrilepis pilosa</i> | 21.3 | 47.0 | 31.7 | S/CSR          | 1836.7                | 40.3     | 35.1                       |
| <i>Afrotrilepis pilosa</i> | 29.7 | 36.0 | 34.3 | CSR            | 4382.0                | 36.7     | 49.1                       |

With LA: Total Leaf Area; SLA: Specific Leaf Area and LDMC: Leaf Dry Matter Content.

C-S-R selection with C= Competitors; S= Stress-tolerators; R= Ruderals

**Table VII.** CSR strategies, following Pierce et al. (2017), for *Microchloa indica*.

| Species                  | C%   | S%    | R%   | Strategy class | LA (mm <sup>2</sup> ) | LDMC (%) | SLA (mm <sup>2</sup> mg <sup>-1</sup> ) |
|--------------------------|------|-------|------|----------------|-----------------------|----------|-----------------------------------------|
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 3.38                  | 35.06    | 1.17                                    |
| <i>Microchloa indica</i> | 1.0  | 99.0  | 0.0  | S              | 40.24                 | 64.64    | 9.18                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 9.47                  | 67.15    | 2.07                                    |
| <i>Microchloa indica</i> | 7.8  | 87.7  | 4.5  | S              | 163.46                | 42.08    | 10.79                                   |
| <i>Microchloa indica</i> | 3.0  | 84.6  | 12.4 | S              | 86.65                 | 57.70    | 14.56                                   |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 10.27                 | 49.17    | 3.97                                    |
| <i>Microchloa indica</i> | 1.5  | 98.5  | 0.0  | S              | 40.09                 | 43.55    | 6.99                                    |
| <i>Microchloa indica</i> | 10.0 | 89.4  | 0.5  | S              | 215.38                | 41.61    | 9.87                                    |
| <i>Microchloa indica</i> | 0.7  | 99.3  | 0.0  | S              | 31.34                 | 40.68    | 4.11                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 4.02                  | 38.89    | 1.68                                    |
| <i>Microchloa indica</i> | 3.0  | 97.0  | 0.0  | S              | 95.45                 | 26.32    | 5.02                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 9.55                  | 42.14    | 3.00                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 7.63                  | 36.90    | 2.72                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 5.37                  | 31.21    | 1.91                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 6.58                  | 28.37    | 1.59                                    |
| <i>Microchloa indica</i> | 4.9  | 75.9  | 19.2 | S/SR           | 218.36                | 71.64    | 23.06                                   |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 7.92                  | 55.49    | 3.86                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 11.43                 | 54.01    | 3.39                                    |
| <i>Microchloa indica</i> | 0.2  | 99.8  | 0.0  | S              | 27.09                 | 66.34    | 7.93                                    |
| <i>Microchloa indica</i> | 0.0  | 100.0 | 0.0  | S              | 13.48                 | 48.97    | 3.33                                    |

With LA: Total Leaf Area; SLA: Specific Leaf Area and LDMC: Leaf Dry Matter Content.

C-S-R selection with C= Competitors; S= Stress-tolerators; R= Ruderals

**Table VIII:** CSR strategies, following Pierce et al. (2017), for *Sporobolus festivus*.

| Species                    | C%    | S%    | R%    | Strategy class | LA (mm <sup>2</sup> ) | LDMC (%) | SLA (mm <sup>2</sup> mg <sup>-1</sup> ) |
|----------------------------|-------|-------|-------|----------------|-----------------------|----------|-----------------------------------------|
| <i>Sporobolus festivus</i> | 5.40  | 94.60 | 0.0   | S              | 101.4                 | 42.7     | 8.2                                     |
| <i>Sporobolus festivus</i> | 1.54  | 98.46 | 0.0   | S              | 40.7                  | 42.8     | 4.5                                     |
| <i>Sporobolus festivus</i> | 4.62  | 95.38 | 0.0   | S              | 96.7                  | 47.6     | 8.7                                     |
| <i>Sporobolus festivus</i> | 3.07  | 96.93 | 0.0   | S              | 59.9                  | 41.8     | 6.1                                     |
| <i>Sporobolus festivus</i> | 5.64  | 94.36 | 0.0   | S              | 131.0                 | 51.3     | 9.2                                     |
| <i>Sporobolus festivus</i> | 7.02  | 80.90 | 12.08 | S              | 243.5                 | 58.2     | 14.7                                    |
| <i>Sporobolus festivus</i> | 3.28  | 96.72 | 0.0   | S              | 77.6                  | 53.6     | 5.9                                     |
| <i>Sporobolus festivus</i> | 10.62 | 80.83 | 8.55  | S              | 221.6                 | 37.2     | 11.7                                    |
| <i>Sporobolus festivus</i> | 2.97  | 97.03 | 0.0   | S              | 62.1                  | 45.2     | 5.5                                     |
| <i>Sporobolus festivus</i> | 4.62  | 95.83 | 0.0   | S              | 116.1                 | 56.7     | 8.1                                     |
| <i>Sporobolus festivus</i> | 3.03  | 96.07 | 0.0   | S              | 62.4                  | 44.6     | 6.1                                     |
| <i>Sporobolus festivus</i> | 1.30  | 98.70 | 0.0   | S              | 47.1                  | 31.9     | 3.8                                     |
| <i>Sporobolus festivus</i> | 6.41  | 86.83 | 6.76  | S              | 162.5                 | 49.9     | 11.7                                    |
| <i>Sporobolus festivus</i> | 7.53  | 87.15 | 5.33  | S              | 146.8                 | 40.0     | 10.9                                    |
| <i>Sporobolus festivus</i> | 7.66  | 92.34 | 0.0   | S              | 154.2                 | 43.0     | 9.2                                     |
| <i>Sporobolus festivus</i> | 3.09  | 96.91 | 0.0   | S              | 57.4                  | 39.5     | 4.2                                     |
| <i>Sporobolus festivus</i> | 15.62 | 76.39 | 7.99  | S/CS           | 361.2                 | 34.6     | 11.5                                    |
| <i>Sporobolus festivus</i> | 4.51  | 95.49 | 0.0   | S              | 70.7                  | 36.1     | 5.2                                     |
| <i>Sporobolus festivus</i> | 6.68  | 82.44 | 10.87 | S              | 183.5                 | 50.1     | 13.3                                    |
| <i>Sporobolus festivus</i> | 4.73  | 92.52 | 2.75  | S              | 109.8                 | 51.0     | 10.5                                    |
| <i>Sporobolus festivus</i> | 9.58  | 80.23 | 10.18 | S              | 241.4                 | 42.4     | 12.5                                    |
| <i>Sporobolus festivus</i> | 2.66  | 97.34 | 0.0   | S              | 66.2                  | 54.8     | 7.9                                     |
| <i>Sporobolus festivus</i> | 5.05  | 94.95 | 0.0   | S              | 101.6                 | 45.6     | 7.5                                     |
| <i>Sporobolus festivus</i> | 14.30 | 68.33 | 17.37 | S/SR           | 329.1                 | 32.6     | 14.0                                    |

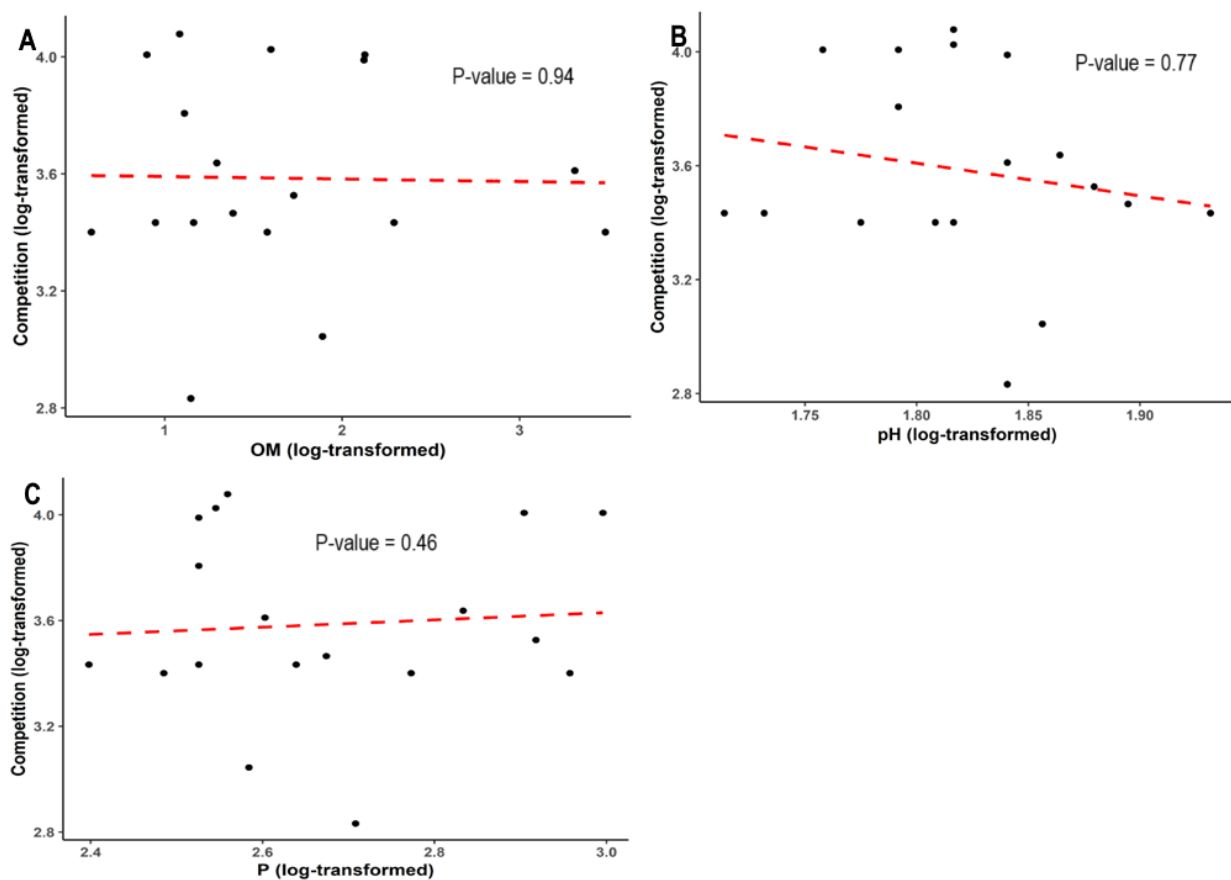
With LA: Total Leaf Area; SLA: Specific Leaf Area and LDMC: Leaf Dry Matter Content.  
C-S-R selection with C= Competitors; S= Stress-tolerators; R= Ruderals

**Table IX.** CSR strategies, following Pierce et al. (2017), for *Tripogonella minima*.

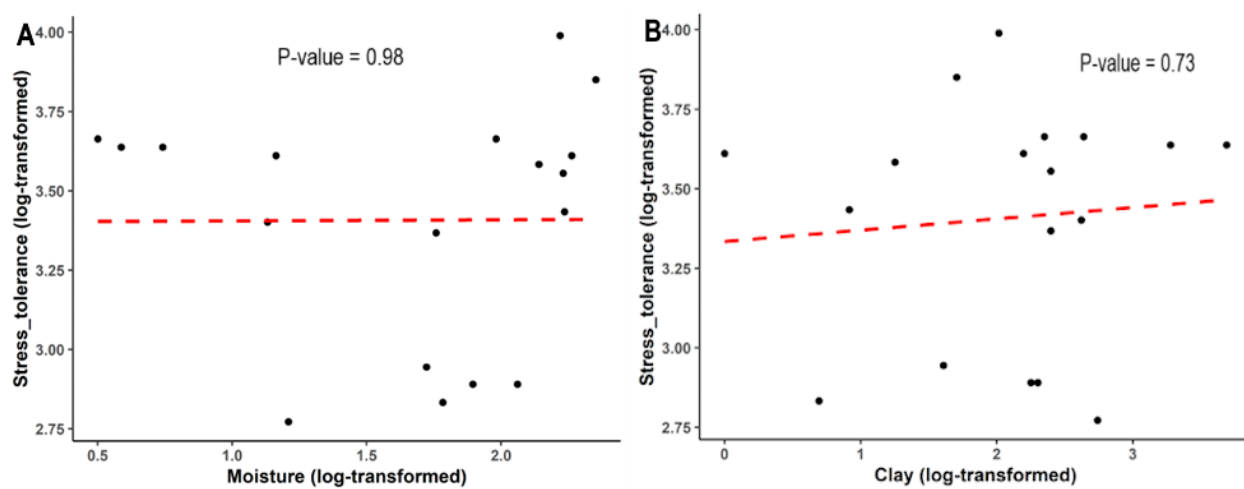
| Species                 | C%  | S%    | R%  | Strategy<br>class | LA (mm <sup>2</sup> ) | LDMC<br>(%) | SLA<br>(mm <sup>2</sup> mg-1) |
|-------------------------|-----|-------|-----|-------------------|-----------------------|-------------|-------------------------------|
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 24.2                  | 62.3        | 6.7                           |
| <i>Tripogon minimus</i> | 0.9 | 99.1  | 0.0 | S                 | 37.3                  | 59.0        | 9.6                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 8.8                   | 75.3        | 4.1                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 23.3                  | 61.2        | 6.3                           |
| <i>Tripogon minimus</i> | 2.2 | 97.8  | 0.0 | S                 | 55.3                  | 52.2        | 5.7                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 11.4                  | 54.5        | 3.8                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 20.6                  | 51.1        | 4.4                           |
| <i>Tripogon minimus</i> | 0.7 | 99.3  | 0.0 | S                 | 33.2                  | 50.4        | 6.6                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 16.2                  | 56.1        | 4.2                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 11.3                  | 54.7        | 3.5                           |
| <i>Tripogon minimus</i> | 7.4 | 92.6  | 0.0 | S                 | 160.1                 | 45.9        | 9.4                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 18.7                  | 57.0        | 5.7                           |
| <i>Tripogon minimus</i> | 2.1 | 97.9  | 0.0 | S                 | 53.2                  | 50.4        | 8.4                           |
| <i>Tripogon minimus</i> | 1.2 | 98.8  | 0.0 | S                 | 38.4                  | 46.2        | 4.9                           |
| <i>Tripogon minimus</i> | 1.9 | 98.1  | 0.0 | S                 | 55.5                  | 59.7        | 9.0                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 10.2                  | 59.0        | 3.3                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 3.5                   | 47.3        | 1.9                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 20.7                  | 62.4        | 5.9                           |
| <i>Tripogon minimus</i> | 1.0 | 99.0  | 0.0 | S                 | 37.8                  | 52.4        | 5.7                           |
| <i>Tripogon minimus</i> | 0.0 | 100.0 | 0.0 | S                 | 14.2                  | 57.4        | 5.1                           |
| <i>Tripogon minimus</i> | 3.2 | 96.8  | 0.0 | S                 | 69.7                  | 48.9        | 6.9                           |

With LA: Total Leaf Area; SLA: Specific Leaf Area and LDMC: Leaf Dry Matter Content.

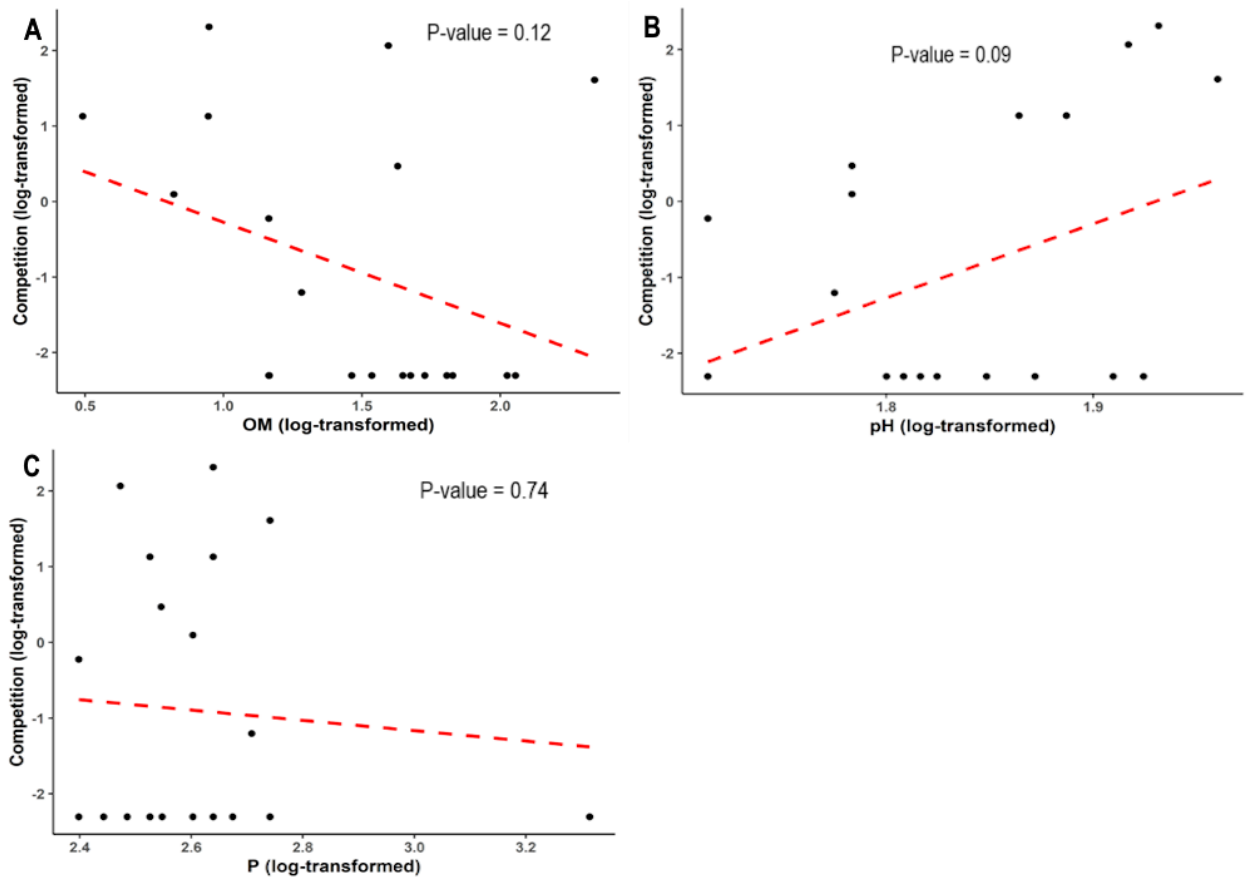
C-S-R selection with C= Competitors; S= Stress-tolerators; R= Ruderals



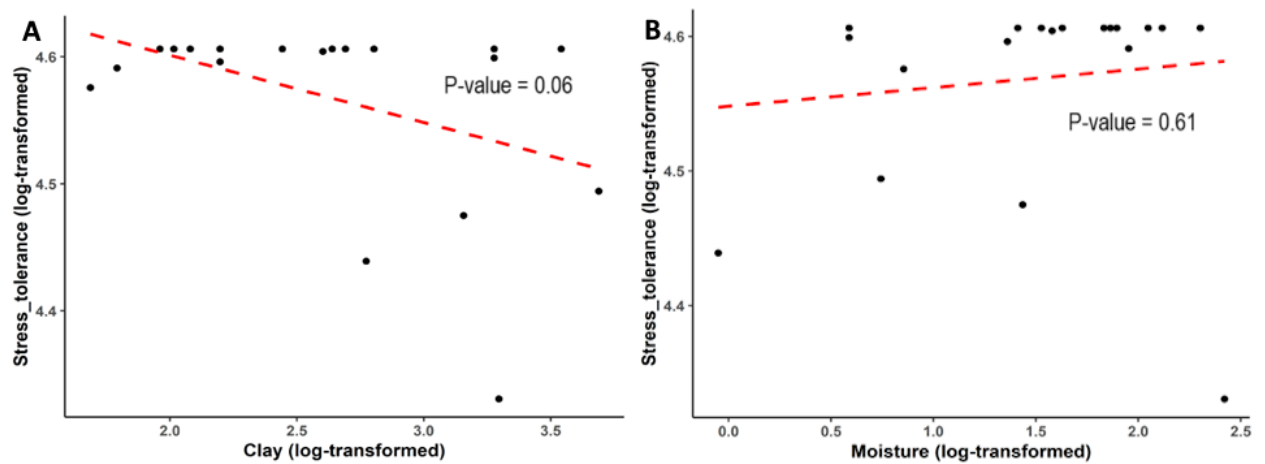
**Figure 39.** Relationship between *soil variables*: **A)** soil organic matter (OM), **B)** pH and **C)** phosphorus (P) and the competitive strategy (C) of *Afrotrilepis pilosa*.



**Figure 40.** Relationship between soil variables: **A)** soil Moisture and **B)** Clay and the stress-tolerance (S) strategy of *Afrotrilepis pilosa*.

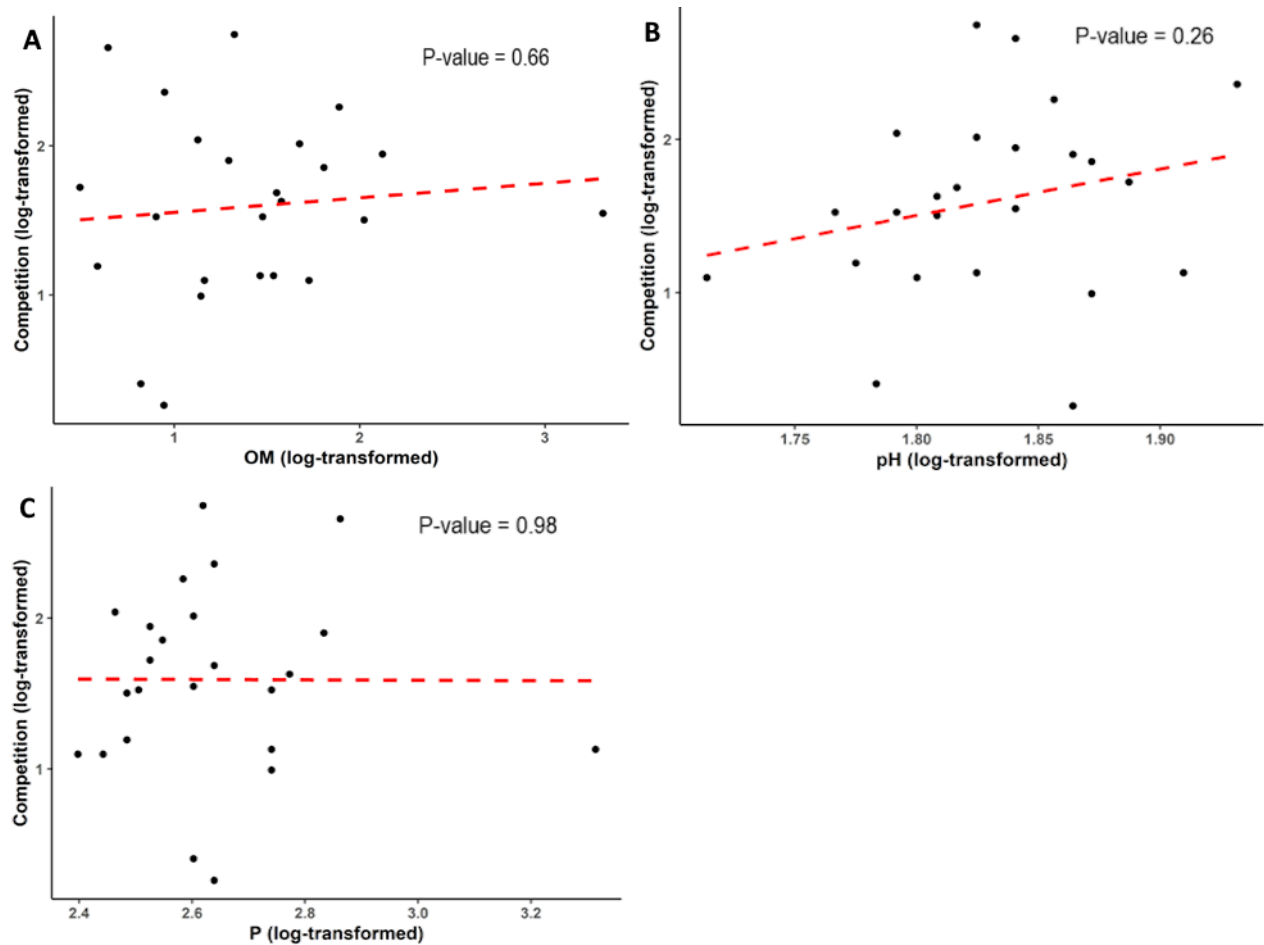


**Figure 41.** Relationship between soil variables: **A)** soil organic matter (OM), **B)** pH and **C)** phosphorus (P) and the competitive (C) strategy of *Microchloa indica*.

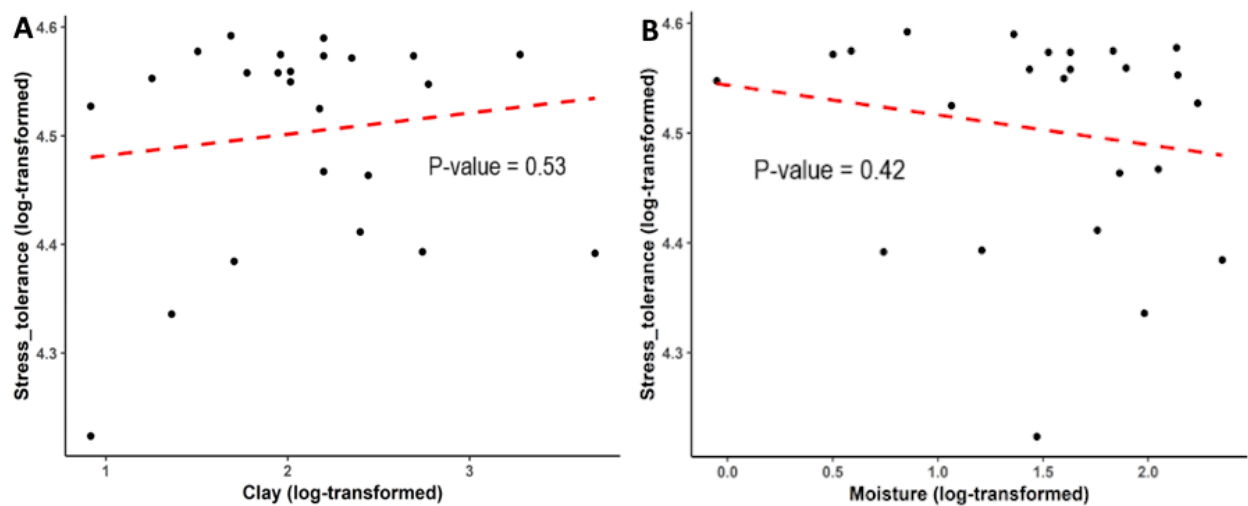


**Figure 42.** Relationship between soil variables: **A)** soil Clay and **B)** Moisture and the stress-tolerance (S) strategy of *Microchloa indica*.

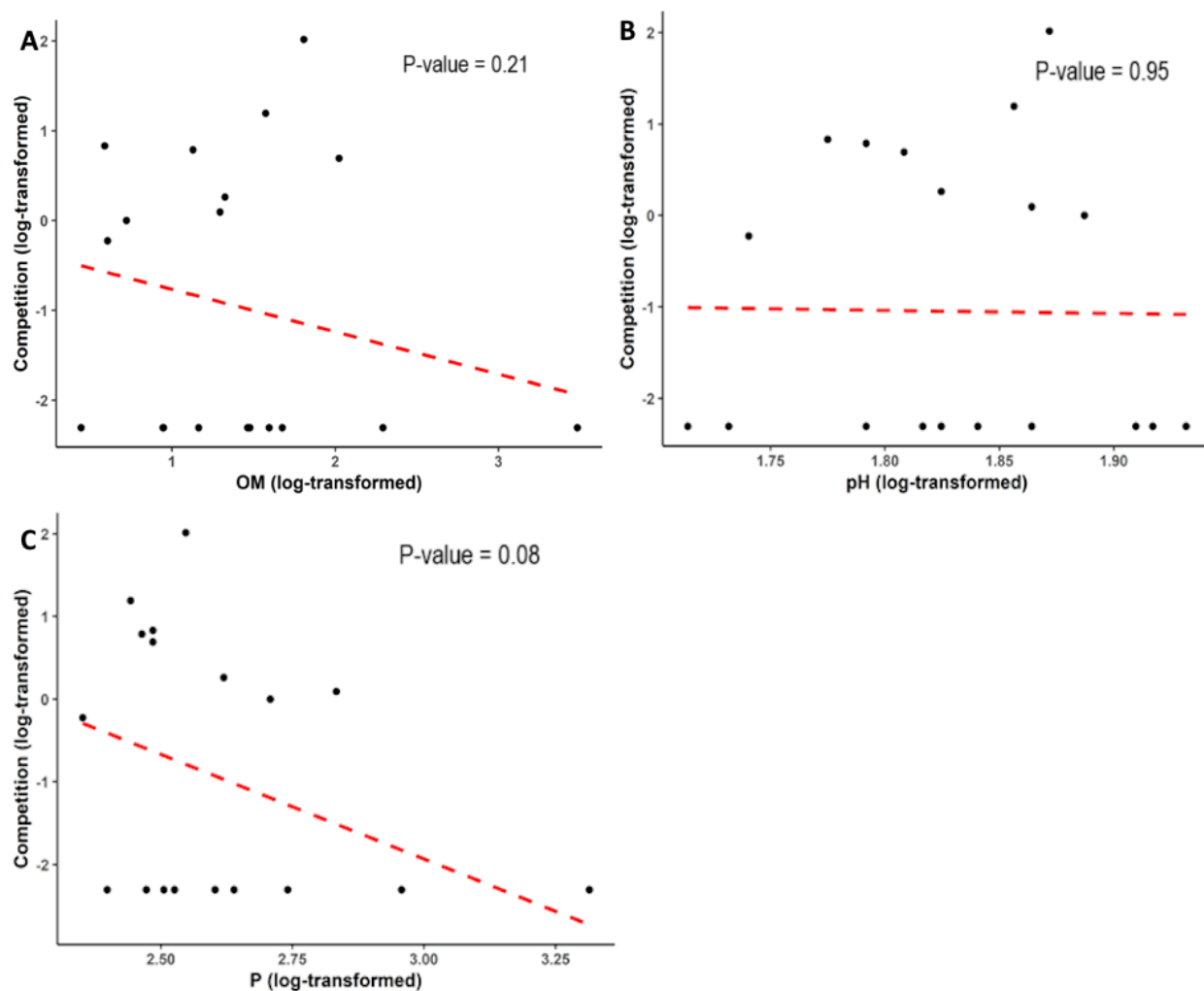




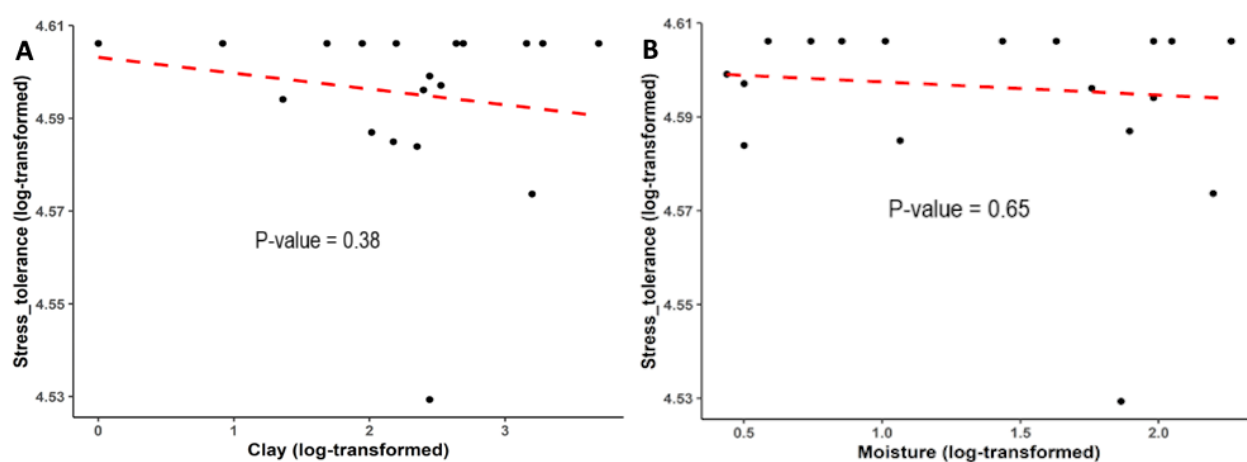
**Figure 43.** Relationship between soil variables: **A)** soil organic matter (OM), **B)** pH and **C)** phosphorus (P) and the competitive (C) strategy of *Sporobolus festinus*.



**Figure 44.** Relationship between soil variables: **A)** soil Clay and **B)** Moisture and the stress-tolerance (S) strategy of *Sporobolus festinus*.



**Figure 45.** Relationship between soil variables: **A)** soil organic matter (OM), **B)** pH and **C)** phosphorus (P) and the competitive (C) strategy of *Tripogonella minima*.



**Figure 46.** Relationship between soil variables: **A)** soil Clay and **B)** Moisture and the stress-tolerance (S) strategy of *Tripogonella minima*.

## Chapter 9: Effects of seed age on desiccation tolerance in DT Plants

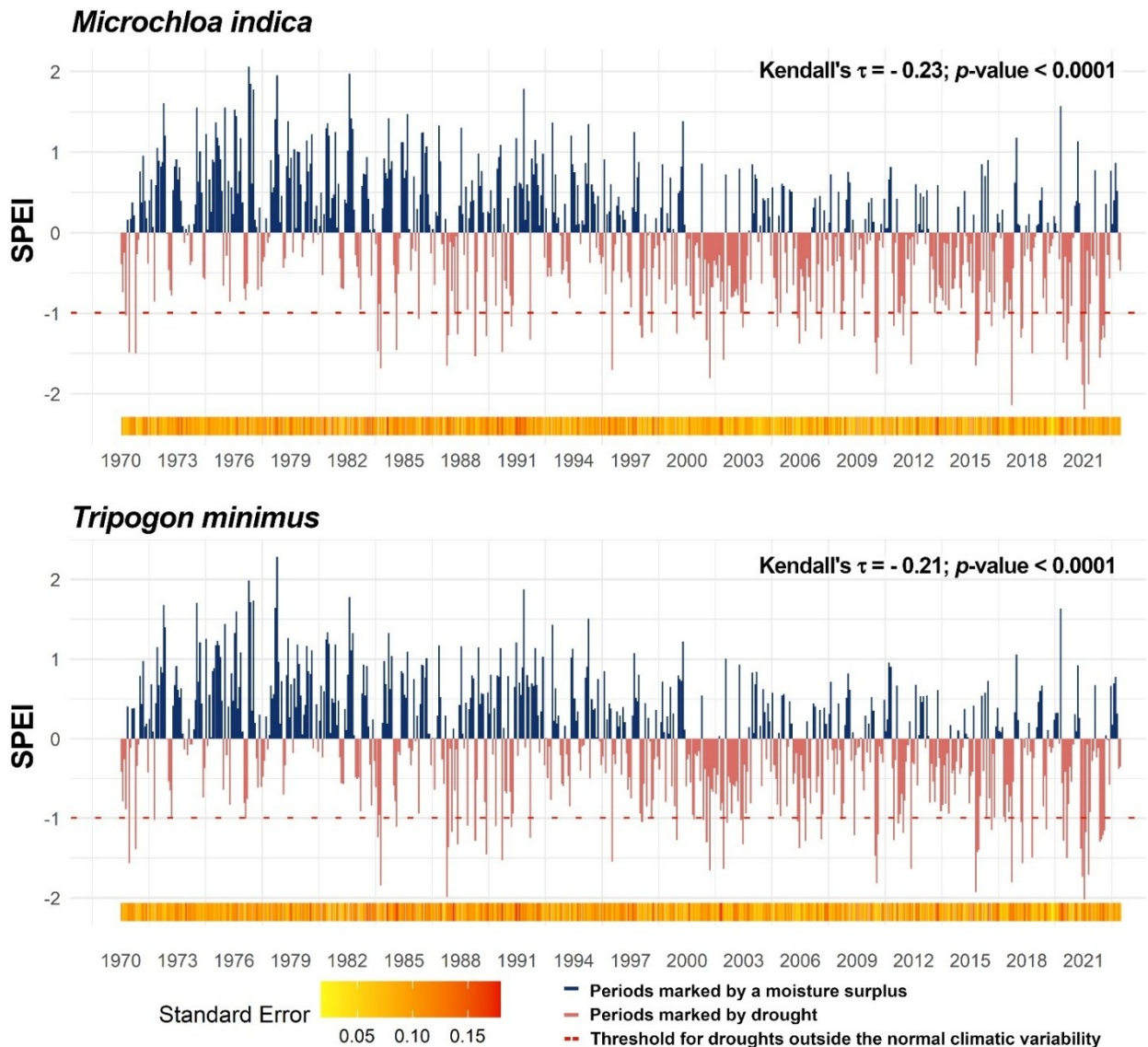
### 9.1. Changes in species exposure to drought owing to climate change

A moderate but consistent increase in exposure was observed for both *M. indica* and *T. minima* to drought (*M. indica*, Kendall's  $\tau = -0.23$  and  $p\text{-value} < 0.0001$ ; while for *T. minima*, Kendall's  $\tau = -0.21$  and  $p\text{-value} < 0.0001$ , Figure 47).

### 9.2. Effect of seed ageing on seedlings' desiccation tolerance across the developmental stages

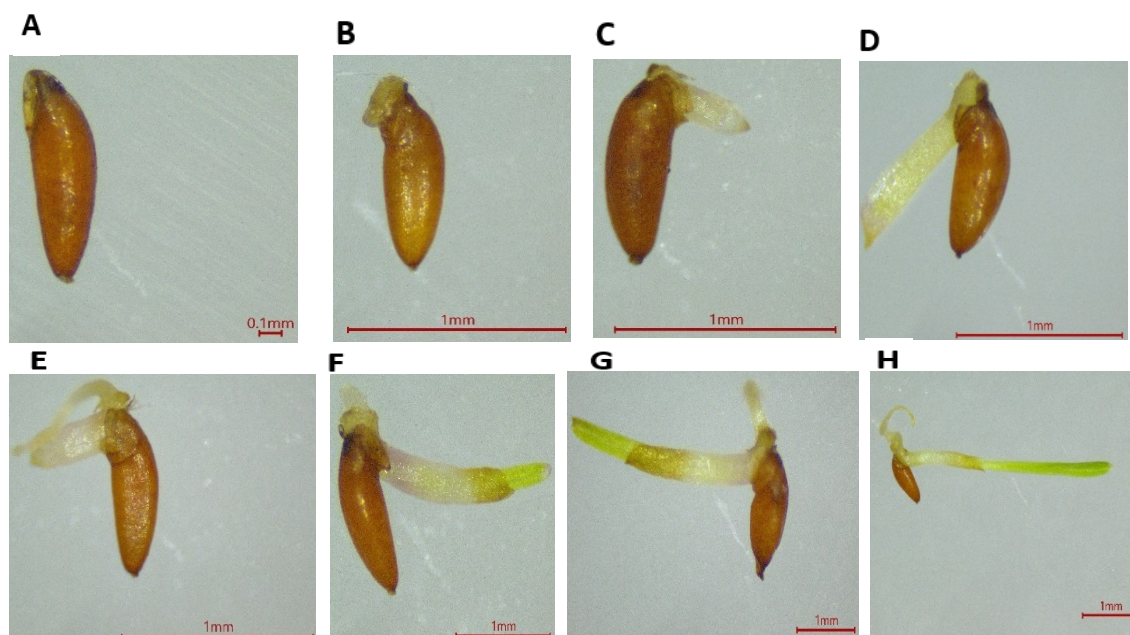
A statistically significant effect of age was observed for the desiccation tolerance ability of *Microchloa indica* seedlings at stage 1 (Estimate = -4.7,  $p = 2.2\text{E-}16$ ) and for stage 7 (Estimate = -2.61,  $p = 3.6\text{E-}5$ ). Seedlings at these stages from older seeds had lower survival rates after the desiccation experiment. However, any significant effect of seed age on the desiccation tolerance ability of *Microchloa indica* seedlings from stage 2 to 6 ( $p < 0.1$ ) was found (Figure 48; Table X). For *Tripogonella minima*, a significant effect of seed age on the seedlings' desiccation tolerance ability was only detected at stage 1 (Estimate = -0.070,  $p = 0.008$ ), where 18 months old seeds had lower survival rates after the desiccation experiment. Stages 2 to 6 (Figure 49) had identical survival rates (100%) across both seed ages, and no significant effects of age were found ( $p = 1.000$ ). From stage 7, seed age had a lower but no significant effect on seedlings, while no effect of seed age was registered in seedlings from stages 2-6.

Figure 50 illustrates the percentages of desiccation tolerance (or survival rate) for seedlings germinated from 6 and 18 months old seeds for *Microchloa indica* and *Tripogonella minima*, across each of the 7 developmental stages. For 6 months old seeds of *Microchloa indica*, desiccation tolerance is maintained from stage 1 to stage 6 with a 100% survival rate, and 99% at stage 7. But, for 18 months old seeds, the curve shows a slightly cascading trend, indicating variation among different stages, with survival rates of 62%, 97%, 100%, 98%, 100%, 98% and 85%, respectively, from stage 1 to stage 7. In contrast, for *Tripogonella minima*, whether for 6 or 18 months old seeds, stages 2 to 6 all show 100% survival. Significant variations occur only at stages 1. While at 6 months of age, *Tripogonella minima* shows 84.66% stage 1, at 18 months, it shows 70%. Overall, the results (Figure 50) show that the survival rate (desiccation tolerance) varies across the developmental stage.

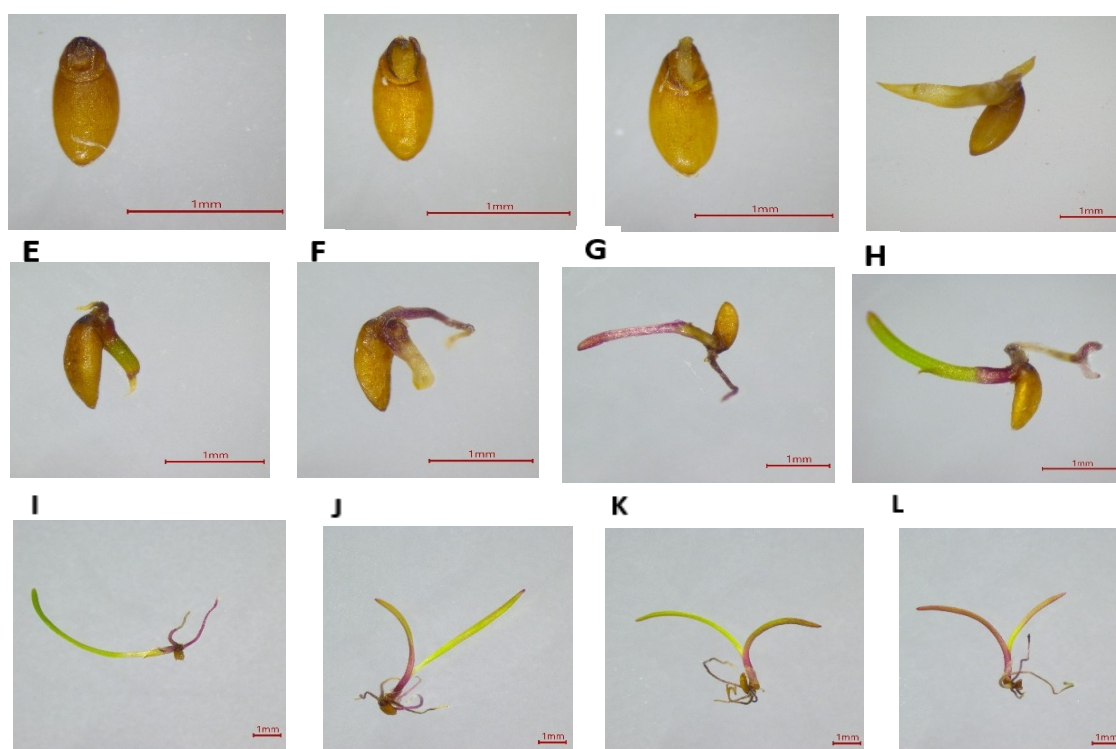


**Figure 47.** Increase in exposure of *Microchloa indica* and *Tripogonella minima* to drought owing to climate change.

The time-series for the period from 1970 to 2022 shows the mean monthly values of the standardized Precipitation Evapotranspiration Index (SPEI) for all occurrence points of each species, while the standard error for each month is shown below the time-series. Droughts are depicted by the negative (Red) SPEI values, and trends are identified by the Mann-Kendall trend test, where statistically significant negative Kendall's  $\tau$  depict a negative trend in SPEI values over time. SPEI values lower than -1 describe droughts outside the normal climatic variability for each locality.



**Figure 48.** Germination and early seedling developmental stages in *Tripogonella minima*. Stage 1: water uptake accompanied by changes in size and shape (A); Stage 2: rupture of the testa (B); Stage 3: protrusion and emergence of the radicle (C); Stage 4: clearly visible emergence of the coleoptile (D); Stage 5: coleoptile elongation and root development, with tissues staining purple (E–F); Stage 6: cotyledon (become photosynthetically active, appearing green) and root, (G); Stage 7: fully developed cotyledon (whole seedling, H).

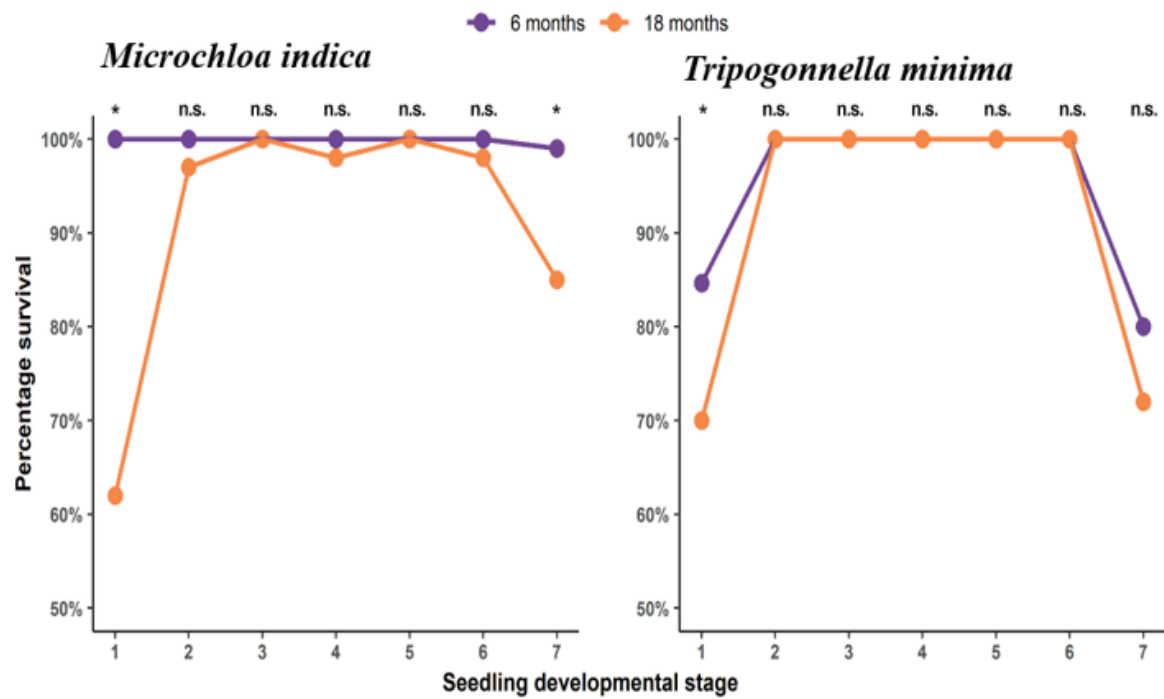


**Figure 49.** Germination and early seedling developmental stages in *Microchloa indica*. Stage 1: water uptake accompanied by changes in size and shape (A); Stage 2: rupture of the testa (B); Stage 3: protrusion and emergence of the radicle (C); Stage 4: clearly visible emergence of the coleoptile (D); Stage 5: coleoptile elongation and root development, with tissues staining purple (E–G); Stage 6: cotyledon (becomes photosynthetically active, appearing green) and root (H); Stage 7: fully developed cotyledon (I); Stage 8: formation of the first leaf, in some cases, a secondary root (J–L).

**Table X.** Effect of seed age and developmental stage on desiccation-tolerance based on a Firth logistic linear model.

| Species                    | Stage | Estimate | Std. Error | p-value     |
|----------------------------|-------|----------|------------|-------------|
| <i>Microchloa indica</i>   |       |          |            |             |
|                            | 1     | -4.97    | 1.43       | 2.2E-16***  |
|                            | 2     | -1.97    | 1.52       | 0.109       |
|                            | 3     | 0        | 2          | 1           |
|                            | 4     | -1.63    | 1.55       | 0.225       |
|                            | 5     | 0        | 2          | 1           |
|                            | 6     | -1.63    | 1.55       | 0.225       |
|                            | 7     | -2.61    | 0.86       | < 0.0001*** |
| <i>Tripogonella minima</i> |       |          |            |             |
|                            | 1     | -0.070   | 0.027      | 0.008**     |
|                            | 2     | 0.000    | 0.167      | 1.000       |
|                            | 3     | 0.000    | 0.167      | 1.000       |
|                            | 4     | 0.000    | 0.167      | 1.000       |
|                            | 5     | 0.000    | 0.167      | 1.000       |
|                            | 6     | 0.000    | 0.167      | 1.000       |
|                            | 7     | -0.036   | 0.026      | 0.167       |

The reference category for the seed age is 6 months and stage 1 for the stages. Significance of codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1



**Figure 50.** Desiccation tolerance ability (depicted by percentage of survival) of *Tripogonnella minima* and *Microchloa indica*, across the different seedling developmental stages at 6 and 18 months old.

\* significant differences between seed age; n.s. - non-significant differences between seed age.



## Chapter 10: General discussion

This study addressed the factors shaping the distribution of desiccation-tolerant vascular plants in West Africa by examining their diversity, spatial patterns, ecological variation, and responses to environmental change.

Chapter 6, which addressed the first objective, documented the diversity, distribution, and conservation status of desiccation-tolerant plants across the region. In total, 49 desiccation-tolerant vascular plant species belonging to 30 genera and 11 families were recorded. Ferns accounted for the majority of species, followed by angiosperms and lycophytes. Species richness was unevenly distributed, with Cameroon, Nigeria, and Côte d'Ivoire harboring the highest numbers of species, and six species were identified as endemic to West Africa. Most species (86%) have not yet been assessed for conservation status, and desiccation-tolerant plants were exposed to multiple anthropogenic pressures, particularly quarrying on inselbergs, with existing protected areas reducing but not eliminating exposure.

Building on this, Chapter 7, addressing the second objective, identified current centers of diversity and endemism concentrated in mountainous and topographically complex regions, including the Guinea Highlands, the Togo Mountains, and the Cameroon Volcanic Line. Species distribution models indicated that most species are projected to experience range contractions under both optimistic and pessimistic climate scenarios, with severe reductions in suitable habitat under late-century SSP5 projections. Only a small proportion of priority conservation areas overlapped with existing protected areas.

At a finer scale, Chapter 8, linked to the third objective, examined the influence of soil on the intraspecific variation in ecological strategies of desiccation-tolerant grasses. It shows that despite the fact that the four species studied exhibited contrasting CSR strategy profiles and variation in leaf traits, no significant relationships were detected between soil characteristics and CSR strategy components.

Finally, Chapter 9, corresponding to the fourth objective, assessed the effects of seed age on desiccation tolerance under changing environmental conditions. The results revealed that exposure to drought increased moderately but consistently for both study species under future climate scenarios and that seed age influenced desiccation tolerance primarily at early developmental stages, while desiccation tolerance remained high and largely unaffected by seed age at later stages.

Building on the results presented above, the following discussion places these findings within the broader literature on desiccation-tolerant plant diversity and conservation.



With respect to the first objective related to diversity, geographical distribution, exposure and conservation status of desiccation-tolerant plants in West Africa, the findings suggest that West Africa harbors relatively low diversity of DT plants compared to the other regions. West Africa and India were found to share some species in common.

The checklist provided by **Smrithy *et al.* (2023)** reveals some biogeographical similarities with the findings of this study, while desiccation-tolerant angiosperms in West Africa are distributed across three monocot families (Cyperaceae, Poaceae and Velloziaceae) and one dicot family (Linderniaceae), the Indian checklist records two monocot families (Cyperaceae and Poaceae) and two dicot families (Gesneriaceae and Linderniaceae). But while in West Africa, mat-forming DT plants are dominated by Cyperaceae (e.g., *Afrotrilepis pilosa*), in India, they are dominated by Poaceae. This aligns with previous studies that reported that rock outcrops across Brazil, Africa and Madagascar are predominantly colonized by Cyperaceae (e.g., genera such as *Afrotrilepis* and *Coleochloa*), Velloziaceae (e.g., genera such as *Vellozia* and *Xerophyta*), and ferns (**Porembski and Barthlott, 2000, 2007; de Paula *et al.*, 2017**).

Cyperaceae is almost absent in India, it is represented only by *Fimbristylis dichotoma*, which has been reported to possess DT properties on Australian outcrops, but its desiccation-tolerant properties in India have not been tested yet. Poaceae richness is far lower in West Africa (10 species, 5 genera) compared to India (30 species, 15 genera). Lycophytes have also shown lower diversity, with West Africa represented by a single *Selaginella* species, while in other tropical regions (e.g., India, Madagascar), Selaginellaceae is more speciose. The relative poverty of DT plants in West Africa could partly be explained by the near absence of Velloziaceae, which is a central family to DT diversity in Brazil and Madagascar (**de Paula *et al.*, 2017**). This family is extensively documented for its desiccation tolerance, with nearly 50 species distributed across four genera: *Barbacenia* with 11 species, *Barbaceniopsis* with 3 species, *Vellozia* with 19 species, mainly in Brazil and *Xerophyta* with 16 species in Africa/Madagascar (**de Paula *et al.*, 2017**). In West Africa, the family is reduced to a single species, *Xerophyta schnitzleinia* (**Owoseye, 1972**).

Another factor is the dominance of *Afrotrilepis pilosa*, this species forms a highly stable and competitive community that suppresses the establishment of other species (**Porembski *et al.*, 1997**). Over time, this stability may have limited opportunities for other species to establish or evolve. For example, **Porembski (1996)** recorded only 15 vascular plant species (DT and non-DT plants) across 100 plots in Côte d'Ivoire. With an exceptional lifespan of up to 200 years (**Bonardi, 1966 in Porembski, 1996**), *Afrotrilepis pilosa* reinforces its dominance over

time. While disturbances like fire may temporarily allow faster-growing taxa to establish, *Afrotrilepis* quickly re-establishes itself, further limiting species richness.

Research on West African inselbergs is also geographically uneven. While countries, like Côte d'Ivoire, Cameroon, Nigeria and Guinea, have been relatively well-studied, particularly regarding DT plants, areas such as the Sahelian zone of Burkina Faso and neighboring regions remain largely under-documented (Müller, 2007). While Porembski *et al.* (2021), noted that DT plants are rarely found in truly arid regions and emphasized the lack of detailed information on their climatic limits, drought frequency and precipitation levels. In areas such as Sahara (Aïr), Anthelme *et al.* (2011) recorded some species having DT properties (e.g., *Actiniopteris radiata*) on rock outcrops, suggesting that these plants may be underrepresented in the current dataset due to limited research, rather than true absence.

This uneven sampling could limit our ability to fully assess the diversity and distribution of DT plants in the region, but also hampers efforts to assess their conservation status, as some might be threatened or endangered. The lack of comparable studies across West Africa could be a factor that can exacerbate this bias (Müller, 2007), making it challenging to generalize findings or draw meaningful comparisons between inselberg vegetation across the region. Future research in West Africa should focus on filling these kinds of gaps by providing a better understanding of inselberg vegetation, particularly DT plants. Expanding surveys and studies, especially in understudied regions, could provide important information on the ecological, evolutionary factors shaping the distribution and conservation status of DT plants.

Only four studies mentioned the need for the conservation of DT plants or their habitats. Two of them focused on the entire plant community (i.e., Porembski *et al.*, 1994; Porembski, 2007) and two others focused on ecological processes and functioning (i.e., Porembski, 2000; Porembski *et al.*, 2016). Even though they are not explicitly targeting DT plants, these studies either highlighted the ecological singularity of a species in the ecosystem DT plants occur (i.e., inselbergs) or acknowledged threats to its biodiversity to claim its need for conservation. However, those studies did not produce enough evidence to justify their claims, even though it was not the aim of any of the mentioned studies to measure species conservation needs to support conservation efforts. However, there is a need for studies that are explicitly designed to assess and discuss the conservation of DT plants.

Conservation initiatives on DT plants would benefit from going beyond general conservation narratives towards a mechanistic understanding of species conservation needs. The vulnerability framework suggested by Dawson *et al.* (2011), is a good starting point to understand the mechanisms that lead DT plants to need conservation action, if they do. Dawson

*et al.* (2011) describe species vulnerability to environmental changes as a result of their exposure (i.e., the magnitude of changes a species undergoes), sensitivity (i.e., how much a species is affected by changes) and adaptive capacity (i.e., how much a species can mitigate the negative effects of environmental changes).

According to this framework, species conservation needs increase under high-level exposure, high sensitivity, and low adaptive capacity. By identifying the importance of each component in the species vulnerability equation (i.e., exposure, sensitivity, and adaptive capacity), conservation initiatives can be more effective by strategically intervening in the critical component for the species in question. For example, assuming that different DT plants in the same community are similarly exposed to a given threat, the species' sensitivity and adaptive capacity to this threat are likely to vary across species. Especially, when considering that DT plants are found in 11 families in West Africa, and desiccation tolerance has independently re-evolved across vascular plants' phylogeny (**Oliver *et al.*, 2000**; please also see Dollo's Law **Gould (1970)**). If attempts to reduce species' exposure to threats fail (e.g., local decision-makers cannot stop climate change effects in a given location), conservation strategies for species with high sensitivity, but high dispersal capacities (i.e., high adaptive capacity) might focus on ensuring species migration to new suitable locations (e.g., increasing the connectivity between protected areas and monitoring species movement and biotic interactions).

However, if the species have high sensitivity and a low dispersal capacity (i.e., low adaptive capacity), more intensive conservation interventions might be taken to ensure the species will not go extinct in the wild (e.g., decision-makers could opt for assisted migration to guarantee that one species will not go extinct in the wild).

Understanding those three components is not always an easy task. Scientists and conservationists might encounter challenges in assessing some components (e.g., species can mitigate the negative effect of changes in many ways, from showing high genetic diversity to dispersing to new suitable areas (**Dawson *et al.* 2011**)), and available resources are insufficient to evaluate every species at the proper time (**Cullen, 2013**). Studies with a focus on communities or their components could attempt to identify species to be prioritized for a posterior mechanistic conservation assessment.

For DT plants, there is an incomplete information about which species require more attention for conservation. Eighty-six percent (86%) of the species recorded have not yet been assessed for conservation under the IUCN Red List framework, as eight countries have not evaluated DT species; aligning with the general underrepresentation of West African plant species in global conservation assessments (IUCN, 2025). Although providing systematic and

conservation-explicit guidelines for species conservation, the IUCN Red List framework might also be costly and time-consuming. For instance, monitoring population size reduction (Criteria A from the IUCN Red List framework) recommends measures over 10 years or three generations (IUCN, 2012). Alternatively, quicker (yet robust) assessments could also be used to inform about priority species for conservation (e.g., Zizka *et al.* 2022; Bachman *et al.* 2024; Cazalis *et al.* 2024) and which species the vulnerability framework from Dawson *et al.* (2011), can be applied to for more effective conservation initiatives.

The studies analyzed had a different approach. Some studies highlighted threats to inselberg species, including DT plants, to justify species conservation needs. Porembski (2000), discussed that stress-tolerant native inselberg species can be outcompeted by invasive species with a better competitive ability. Invasive species will only establish themselves in a new community if they either have plant responses that confer greater fitness under local environmental constraints (i.e., “trying harder” strategy) or similar fitness when compared to that of local species (i.e., “joining the locals” strategy (Tecco *et al.*, 2010, but see also Chesson, 2000). That means that in ecosystems in which environmental stress is supposed to be the strongest ecological constraint, such as inselbergs, invasive species must either be fit enough to overcome environmental stress compared to local species or at least similarly fit to avoid being excluded by local species. Otherwise, the impact of an alien species would simply be overestimated with neutral (or even positive) effects on the existing community (Davis *et al.*, 2011; Moro *et al.*, 2012).

We argue that invasive species with a better competitive ability would only be a threat in inselbergs if human pressures led to a shift in the importance of different ecological constraints. For example, over-visitation by humans or the introduction of grazing animals in inselbergs might intensify disturbance events (i.e., any external constraint that causes partial or total biomass loss; sensu Grime (1977) and reduce the relative importance of environmental stress (i.e., any external constraint that reduces plant productivity; sensu Grime (1977)) in shaping inselberg plant communities. This shift would lead ruderal invasive species to exclude native species using the “trying harder” strategy because they are fitter under such new conditions (e.g., de Paula *et al.*, 2015). Thus, new studies that focused on ecological processes that either monitor trends in species populations or habitat shifts over time with the presence of a potentially invasive species (e.g., Kumschick *et al.*, 2015) or assess the changes in functional traits among native species due to the presence of newcomers (e.g., Dehling *et al.*, 2018) must be supported. For DT plants, such studies could advance discussions about the invasiveness of inselbergs and their impact on DT plants.

Another common reasoning to justify the conservation needs of inselberg species, including DT plants, is that many plants exhibit particular responses to environmental challenges (e.g., “specializations” or “adaptations”) and that they have a restricted distribution (e.g., sometimes endemic to inselbergs). These two factors might reinforce the need for monitoring such species or ecosystems. However, there is not enough justification to prioritize a species for conservation.

Concerning the particular responses to environmental challenges, such responses might also be beneficial to cope with some anthropogenic drivers of biodiversity loss. Desiccation tolerance allows for plants to overcome droughts with little or no biomass loss. If drought events become more frequent, intensive and extensive owing to climate change, and thus lead plants to experience high dehydration or desiccation rates, one might logically argue that DT plants are not as sensitive to climate change as desiccation-sensitive plants.

Regarding species-restricted distribution, the expectancy of higher extinctions risks for these species is often related to their narrow niche breadths unfolding a lower tolerance to changes and small population sizes, pushing species close to the viable population thresholds (i.e., minimum number of individuals required for the species to not go locally extinct (**Brown, 1984; Johnson, 1998**)). However, niche is not the only constraint to species distribution patterns (dispersal is also an important cause of the species restricted distribution). This means that species with restricted distribution are not necessarily sensitive to changes. Moreover, the species might be rare on a regional scale, but dominant on a local scale (**Violle *et al.*, 2017**), so they are not close to the viable population thresholds.

For instance, despite *A. pilosa* being endemic to West Africa and restricted to inselbergs, it can be present in very distinct environmental settings (e.g., locations where annual precipitation varies from less than 1000 to more than 3000mm (**Zokov, 2024**)) and achieve high abundances within local communities (**Porembski and Barthlott, 1996**). A species might indeed require conservation attention, but not necessarily because they have particular responses to the environment or because they have restricted distribution.

More lines of evidence are needed to evaluate species’ conservation needs rather than simply relying on clues that, despite their usefulness, may not appropriately describe species’ vulnerability to the anthropogenic drivers of biodiversity loss. However, particular responses to environmental challenges (i.e., desiccation tolerance in this study context) and restricted distribution are appealing features of DT plants and can possibly be used to encourage conservation awareness about DT plants. For example, the three Red Listed species *A. aethiopicum*, *C. domensis*, and *C. yaundense* could play an important role as Cinderella species

in the context of DT plants in West Africa. *C. yaundense* is an inselberg endemic species found only within the urban area of Yaounde (the capital of Cameroon).

Cinderella species are a type of surrogate species (i.e., species that are strategically used by conservation initiatives to promote the conservation of other species (**Smith *et al.*, 2012**) that are endangered, and despite not being as famous as flagship species, have enough charisma or public appeal to improve support on conservation initiatives (**Simberloff, 1998; Smith *et al.*, 2012; Moynes *et al.*, 2021**). These three species could be used in coordination to better capture the phylogenetic and ecological diversity specific to each area (e.g., as flagship fleets; see **Williams *et al.*, 2000; Mazel *et al.*, 2018**). However, raising public awareness of plant species is trickier than for animals, but not an impossible task (**Balding *et al.*, 2016**).

Alternative solutions should not be neglected, such as using umbrella species (i.e., another type of surrogate species, but which are more common features in the landscape, thus more likely to have stronger connections with local communities (**Lambeck, 1997; Caro *et al.* 1999**), or other plant or animal species that occur on rock outcrops and would help conserving DT plants (since many DT plants are associated with these ecosystems). Moreover, surrogate species in conservation initiatives risk failing to solve complex problems through simplistic solutions (**Murphy *et al.* 2014**). Future studies are still necessary to select appropriate surrogate species and evaluate if such strategies satisfy local ecological realities.

The species with more exposure to anthropogenic threats to biodiversity (i.e., *C. yaundense* and *M. squamosa*) are the ones not included in the existing protected area networks. This pattern is especially worrying when considering that they are the two rarest species in our study, as this feature is linked with greater extinction risks (**Lawton, 1993; Flather *et al.*, 2007**). Moreover, while *C. yaundense* is classified as vulnerable by the IUCN, *M. squamosa* is currently unevaluated by the IUCN, hindering the understanding about the conservation needs of one of the species that might most require our attention.

The Aichi Target 11 of the Convention on Biological Diversity (**Flather *et al.*, 2007**) aimed to protect at least 17% of terrestrial areas by 2020 in an equitable and ecologically representative way (and 30% by 2030 according to Target 3 of the Kunming-Montreal Global Biodiversity Framework, **CBD, (2011-2020)**). However, despite the 17% threshold reached in 2024 (**UNEP-WCMC, 2024**), the results show that ecological representativeness has not yet been met. It is estimated that nearly 60% of vascular plant diversity hotspots still remain outside protected areas, leaving many endemic and vulnerable species unprotected despite international conservation targets (**Daru, 2024**). Reducing the protection bias towards certain

ecosystems and species requires the adjustment of conservation objectives to explicitly include overlooked species, such as *C. yaundense* and *M. squamosa*.

However, simply assigning protection areas might not be sufficient to ensure species protection against the anthropogenic drivers of biodiversity loss. In this study, the protected areas may have provided effective buffering against the direct effects of human activities such as quarrying. However, they were less effective in mitigating the indirect effects of human activities such as climate change. For instance, species like *O. aristatum* and *P. scolopendria* had their exposure to quarrying reduced to zero in the protected areas, but had roughly the same level of exposure to climate change when comparing the protected and unprotected inselbergs (in some future scenarios, their level of exposure to climate change was higher in protected areas). Thus, the reasoning for using protected areas to reduce quarrying rates is more straightforward. By establishing protected areas, quarrying activities can be avoided in quarrying-prone areas, which are often neglected by conservation initiatives (**Porembski *et al.*, 2016**), and in which, species often have small geographic ranges (**Torres *et al.*, 2022**).

Mitigating the impacts of quarrying may demand stricter land-use regulation and site-level protection. For example, some species were found on inselbergs included in a protected area, but with evidence of quarrying. Expanding the protection areas that include inselbergs and satisfy the conservation objectives (e.g., 30% under protection by 2030) requires enough resources to ensure the protection of established protected areas.

It is not the responsibility of researchers to find solutions for resource mobilization, but future studies on the conservation of DT plants could provide more evidence on the effectiveness of different conservation approaches to support resource mobilization campaigns, as recommended by the Analysis of the Strategic Plan 2011-2020 of the Convention on Biological Diversity (**Timpte *et al.*, 2018**).

Alternatively, protected areas should be planned more strategically when considering climate change. For example, climate change should not be expected to be stopped by demarking a protected area, although using protected areas to establish dispersal corridors for species' possible migration is a more realistic strategy. There is a non-linear negative relationship between habitat loss and the persistence of species, which requires a habitat of minimal size and structure to maintain viable populations (**McIntyre *et al.*, 1999; Desmet, 2018**). That is, a species' probability of persistence gradually decreases with habitat loss until the connectivity among the remaining habitat patches in which a species exists reaches a point of no return for species persistence (**Desmet, 2018**). Here, habitat connectivity depends on

factors, such as patch size and its spatial arrangement, besides how species interact with the landscape (Keitt *et al.*, 1997; Desmet, 2018).

Conservation planning that can cope with climate change can provide a better understanding of how habitat loss owing to climate change threatens species persistence. Future studies could evaluate the impact of inselberg size and isolation in species metapopulations as to assess the capacity of species to keep gene flow across different inselbergs. Ensuring connectivity among habitat patches where DT plants exist effectively is certain to combat other anthropogenic threats, but it should be more explicitly established as one of the protection area objectives against climate change.

This study considered only exposure to anthropogenic threats, offering a partial picture of species vulnerability. The fact that the two most exposed species are the most rare and unprotected ones should raise our awareness, but it is noteworthy to mention that high-level exposure does not necessarily translate into higher extinction risks. For example, although highly exposed to climate change, *O. aristatum*, an annual species, might be able to complete its life cycle before extreme climatic conditions and escape, to some extent, the negative effects of climate change. On the other hand, species might face high extinction risks even under modest exposure due to their narrower ecological tolerances (Dickinson *et al.*, 2014).

For instance, most Hymenophyllaceae species occur as epiphytes in moist forests and are often sensitive to changes in the desiccation rate due to the lack of mechanisms to reduce water loss (e.g., lack of cuticles, Carriqui *et al.*, 2025). Alternatively, different anthropogenic threats can act in combination, causing additive effects on each other and intensifying their impact on species (Jaureguiberry *et al.*, 2022). Moreover, only the two anthropogenic threats were used as proxies for the different drivers of biodiversity loss. For instance, *M. indica* showed the least exposure to climate change, but its broader occurrence across different ecosystems might expose this species to threats that inselberg-endemic species are not subjected to.

Lastly, it is important to advocate for future studies that not only use multiple lines of evidence to assess species vulnerability, but that also encompass a greater array of threats (e.g., direct exploitation and invasive alien species) to improve our understanding of species conservation needs and support efficient conservation initiatives.

In the context of climate change, the results further highlight that there is a need of the inclusion of DT plants into future conservation studies and efforts. Firstly, as expected, the magnitude of the effects of climate change on species distribution is predicted to be higher under more pessimistic climate scenarios. But the consistent high impact of climate change on



species distribution range in the farthest future of the most pessimistic scenario (i.e., 2071-2100, SSP5) is very alarming.

Thirty-three out of 42 species (78% of DT plants from West Africa) are predicted to exhibit a habitat loss exceeding 75% of their current distribution areas. Some of these species are predicted to go extinct owing to climate change in the farthest future of the most pessimistic scenario. This is the case of *Craterostigma yaundense*, *Cheilanthes inaequalis*, *Pellaea dura*, *Tripogon multiflorus* and *Xerophyta schnizleinia*, and the ultimate need for monitoring these species in West Africa is underscored.

The concerns about these species are even more critical when considering that, even when adopting a globally more sustainable development (i.e., SSP1, which assumes global cooperation between countries and a focus on human well-being), the impact of climate change on DT plants cannot be able to be reversed. Thirty-seven out of 42 species (88% of DT plants from West Africa) will still be negatively impacted by climate change in the farthest future of the most optimistic scenario (i.e., 2071-2100, SSP1), with some species being more critically impacted by it. For example, *Cheilanthes inaequalis* is predicted to go extinct, despite a utopian shift in human practices to reduce human-driven changes in the climate.

We also recommend that conservation studies and efforts focus on species conservation needs, instead of focusing on specific taxonomic groups or species distribution ranges. By affecting many species, climate change is likely to affect a large array of ecosystem functions and services, especially considering that species number is expected to correlate positively with functional diversity (**Tilman *et al.*, 2014; Brown and Anand, 2022**). Besides, these species belong to taxonomic groups with different evolutionary histories and threats to phylogenetic diversity also threaten the evolutionary potential of DT plants in West Africa (i.e., because evolutionary potential increases with phylogenetic diversity; **Winter *et al.*, 2013**). That is, loss of phylogenetic diversity results in the loss of species' potential to evolve, as their populations adapt to environmental changes (**Hall, 1999**), and conservation attention to different taxonomic groups could reduce the risks of losing functional and phylogenetic diversity of DT plants.

It might also feel tempting to scientists and conservationists to focus mostly on the conservation of species with small distribution ranges. Species with smaller distribution ranges are expected to be more sensitive to environmental change due to their narrower niche breadth (**Gaston, 1996; Saupe *et al.*, 2015**), but it is also important to note that anthropogenic drivers can cause the rarity of species, regardless of other constraints to species distribution range (**Fiedler and Jain, 1992**).

Climate change is predicted to affect DT plants with both small and broad distribution ranges. The large impact of climate change will also produce the fragmentation of species' remaining distribution areas. That means that populations of species with both small and broad range sizes will remain in small, suitable patches. The problem is that small patches cannot support a greater number of individuals (i.e., lower carrying capacity; **MacArthur and Wilson, 1967; Hanski, 1998**), and populations in these patches become more prone to local extinction due to demographic and environmental stochasticity (**Fahrig, 2003; Ovaskainen and Hanski, 2004**).

Besides, habitat fragmentation is often followed by the loss of connectivity between populations, reducing the likelihood of immigration of individuals to avoid local extinctions (e.g., through a rescue effect; **Haddad et al., 2015**).

For example, both *Asplenium stuhlmannii* and *Tripogonella minima* are widely distributed in 2 large disjunct areas in West Africa. In the farthest future of the most pessimistic scenario, they are projected to lose up to 94% and 98% and have their distribution range shrunk to multiple small patches very distant from each other.

Yet, even though not exclusively, species with smaller distribution ranges must be prioritized for conservation because their populations are likely to be already found close to patch size thresholds to maintain viable populations. For instance, both *Asplenium monanthes* (the species with the smallest distribution range in our analysis) and *Sporobolus festivus* (widely distributed in West Africa) are predicted to lose up to 89% of their distribution areas. However, this number represents a remaining distribution area of 167 km<sup>2</sup> for *Asplenium monanthes*, which is critically smaller than the remaining distribution area of 221878 km<sup>2</sup> for *Sporobolus festivus*. Not only that, but climate change will also promote the local extinction of *Asplenium monanthes* in continental parts of West Africa, leaving the species to only be found on Bioko Island. Such concerns must be extended to endemic species that could not be evaluated due to the limitations of our methodology (*Afrotrilepis jaegeri* and *Coleochloa domensis*). Species with small distribution areas certainly deserve to be closely monitored to avoid possible extinctions in West Africa. Besides, the inclusion of species with broader distribution ranges in conservation assessments would also allow us to identify species with higher conservation needs and draw more effective conservation strategies.

The priority areas for the conservation of DT plants (i.e., Guinea Highlands, the Togo Mountains, the Cameroon Volcanic Line, and the region spanning from central Cameroon to continental Equatorial Guinea) also accumulate a disproportional diversity and endemism of vascular plants (**CEPF, 2000; Myers et al., 2000; Barthlott et al., 2005; Kier et al., 2009; Cai et al., 2023**).

However, despite their importance, they do not receive the appropriate conservation attention. For instance, only 11% of the priority areas for the conservation of DT plants are found in currently protected areas. This percentage is especially low when considering that these locations will either lose many species or show an increase in endemism richness due to species distribution area contractions owing to climate change. For example, the Guinea Highlands, which currently exhibit a high species richness of DT plants, are predicted to harbor only a low species richness in the farthest future of the most optimistic scenario.

On the other hand, the terrestrial parts of the Cameroon Volcanic Line are predicted to play an important role as an ecological refuge against climate change, maintaining a high species and endemism richness of DT plants even under the pessimistic climate scenarios. That means that key regions for the conservation of DT plants in West Africa (because of their high species and endemism richness, and either an excessive species loss or their role as a refuge), are still below the Aichi Biodiversity Targets to 2020 (i.e., Target 11 which aimed at least 17% of protected areas by 2020) and distant to the Aichi Biodiversity Targets to 2030 (i.e., Target 3 of the Kunming-Montreal Global Biodiversity Framework, which aimed at least 30% of protected areas by 2030; **Convention on Biological Diversity, 2025a; 2025b**).

While increasing the number of protected areas is very much needed, the results shed light on the problem that many current protected areas are not effectively managed. For instance, Mount Cameroon (within the Cameroon Volcanic Line) is included in the priority areas for the conservation of DT plants and benefits from legal protection. However, despite Mount Cameroon National Park having been established in 2010, it does not yet have its boundaries fully defined or sustainable management strategies implemented (**Bergl *et al.*, 2007; Forboseh *et al.*, 2011**). This is problematic because this very strategic area for biodiversity conservation is left susceptible to ongoing exploitation (**Bergl *et al.*, 2007; Forboseh *et al.*, 2011**). In this case, the protection of climate change refuges for DT plants is likely to be threatened by other anthropogenic drivers, increasing the extinction risks of these species. This situation is not exclusive to Mount Cameroon. Even when protection exists, the enforcement is weak and the management is poor due to unclear legal boundaries or minimal conservation activities (**Blom *et al.*, 2004; Oates *et al.*, 2004; Bergl *et al.*, 2007; Cronin *et al.*, 2014**).

It is noteworthy to mention that most centers of diversity and endemism for DT plants in West Africa were related to mountainous regions. This fact reinforces the need for higher protection of these areas. For example, one of the explanations for high species richness in mountains is their topographic complexity, which can produce enough environmental heterogeneity (e.g., variations in climate and soil conditions) to support many species in small

geographic areas (Körner, 2007; Stein *et al.*, 2014; Harrison and Noss, 2017; Rahbek *et al.*, 2019). It means that mountains can harbor more DT plant species and that these species can cope with different environmental challenges. This links taxonomic and functional diversity (e.g., more species which are ecologically more distinct from each other; Tilman *et al.*, 2014; Stark *et al.*, 2017), and preserving functional diversity is crucial to the maintenance of ecosystems' functions and services (Laureto *et al.*, 2015; Brown and Anand, 2022).

Besides, mountains concentrate a great number of species with small distribution ranges. These species exhibit a small distribution range because they have a narrow niche breadth and/or a lower dispersal capacity (Gaston, 1996). That means that species with small distribution ranges are more sensitive to climate change and less likely to perform long-distance dispersal events. Due to mountains' topography creating environmental gradients, one might expect that these species will migrate up or downhill to track new suitable habitats. But there is no guarantee the species will successfully do so, as there is a risk losing species that do not occur anywhere else. This could be the case of *Asplenium aethiopicum*, a vulnerable species according to IUCN Redlist of Threatened Species (IUCN, 2025), which mostly occurs in such mountainous regions in West Africa. To monitor these species' populations is essential to avoid the loss of these species.

It should also be good to keep in mind that many DT plants occur in lowland inselbergs, considered centers of diversity for DT plants by Porembski and Barthlott (2000). With lower elevations than mountains, lowland inselbergs do not produce enough environmental gradient to allow species to move to different altitudes, and a whole inselberg might become unsuitable to species due to climate change.

Besides, our results suggest that lowland inselbergs might be subjected to a greater exposure to climate change and might not play a role as climate change refuges to DT plants. This can be exemplified by the local extinction of *Craterostigma yaundense* and *Xerophyta schnizleinia*, which are mostly related to lowland inselbergs in West Africa. Managing ecological processes in protected areas, rather than solely protecting these areas (see Fiedler and Jain 1992), could be the solution to minimizing the effects of climate changes in those areas.

Ensuring suitable conditions in lowland inselbergs can be important, not only for the persistence of species, but also to keep ecological corridors (e.g., as stepping stone patches) that allowing species to track new suitable locations under unavoidable climate change scenarios. But other factors (e.g., velocity of climate change, species dispersal limitations, and negative biological interactions) must still be better understood before the implementation of strategies seeking the management and landscape integration of lowland inselbergs.

Due to the limitations of the scale of the study did not take into account the existence of microclimatic conditions that could buffer the negative effects of climate change on local species populations. Future studies could, for example, evaluate how the topographic complexity of lowland inselbergs contributes to decouple some habitats (e.g., clefts and crevices or monocotyledoneous mats; **Porembski *et al.*, 2007**) from large-scale shifts in climate and lessen the impact of climate change on DT plants.

Another factor that is also important to consider is that other anthropogenic drivers of biodiversity loss (e.g., land-use change or alien invasive species) could interact with climate change in additive ways (**Jaureguiberry *et al.*, 2022**), and intensify its effect on DT plants' diversity. Those factors could make our findings to be over- and underestimated, respectively. More comprehensive understanding of climate change is an ultimately necessary step to support effective conservation efforts on DT plants in West Africa.

While climate change is expected to strongly influence the future distribution and diversity of DT plants at broader spatial scales, local environmental factors also play a key role in shaping species responses. In particular, soil properties can modulate plant performance and ecological strategies within species. In this context, among the four studied grasses, *Afrotrilepis pilosa* exhibited markedly greater intraspecific variation in CSR strategies compared to the other desiccation-tolerant (DT) species. While *Tripogonella minima*, *Sporobolus festivus*, and *Microchloa indica* were almost entirely stress-tolerant (S) in strategy (>90% of individuals), *A. pilosa* displayed a mixed profile, only 11.1% pure S, with the majority adopting CSR (55.6%) or C/CSR (33.3%) strategies. This broader distribution in trait space suggests a wider functional niche (**Boulangeat *et al.*, 2012**) and higher ecological flexibility, enabling certain species like *A. pilosa* to exploit more favorable microsites or respond dynamically to fluctuating resources.

In inselberg habitats, where microsite variation in slope, soil depth, and water availability can be extreme over very short distances, such flexibility may reflect a capacity to track fine-scale environmental gradients and capitalize on transient resource pulses (**Porembski, 2007; Scarano, 2009**). This aligns with evidence from other stress-prone ecosystems where species with broader functional niches maintain higher performance across heterogeneous microsites (**Violle *et al.*, 2012**).

Thus, *A. pilosa*'s CSR variation may emerge not from soil properties per se, but from interacting effects of micro-environmental heterogeneity, phenotypic plasticity, and the ability to persist in both resource-poor and disturbance-prone patches. In contrast, the three predominantly S-selected species appear highly canalized, displaying strong trait convergence

on resource-conservation strategies. Their near-uniform stress tolerance suggests limited plasticity in response to fluctuating conditions, consistent with the expectation that in extremely stressful environments, high survival depends on a narrow set of conserved traits (**Grime, 2001**).

This pattern mirrors findings from other desiccation-tolerant taxa, such as *Myrothamnus flabellifolia*, which maintain highly conserved stress-tolerance traits across wide edaphic and climatic gradients (**Farrant and Moore, 2011**). Desiccation-tolerant plants on inselbergs (e.g., *Afrotrilepis pilosa*, Cyperaceae mats) are specially adapted to survive extreme, rapidly fluctuating environments. Their persistence across varied substrates suggests that trait–soil links may be relatively weak within this constrained niche (**Alcantra et al., 2015**).

Consistent with this, studies on *M. flabellifolia* have shown that while desiccation tolerance remains extremely high and uniform across sites, variation occurs mainly in growth and reproductive traits, indicating that soil variation is secondary to intrinsic tolerance mechanisms (**Farrant and Moore, 2011; Marks et al., 2022**). Similarly, in *A. pilosa*, observed CSR variation is likely shaped more by micro-environmental heterogeneity, phenotypic plasticity, and disturbance regimes than by average soil properties. Together, these observations support the idea that in highly stress-tolerant species, functional trait variation primarily reflects responses to local microsite conditions and external pressures rather than edaphic gradients.

Disturbance regimes, such as grazing, trampling, or fire, are well known for reducing the dominance of S-selected species and promoting intermediate or ruderal components by inducing a shift in the CSR strategies (**Pierce et al., 2017; Wu et al., 2023**). On inselbergs, where environmental stress is usually the dominant ecological constraint (**Porembski, 2007**), variation in strategies is more likely to arise when other constraints, such as disturbance, become more influential (**Grime, 1977, 2001**).

It should be kept in mind that disturbance does not necessarily mean or replace stress as the primary filter, but can relax its selective pressure, allowing a broader spectrum of strategies to be expressed within populations. The observed CSR variation of *Afrotrilepis pilosa* likely reflects responses to spatially heterogeneous disturbances rather than edaphic gradients.

For instance, intraspecific CSR variation can be strongly influenced by fine-scale environmental heterogeneity and disturbance, even when overall stress tolerance is high. Among highly stress-tolerant species, variation in microsite conditions, such as differences in shade, water retention, or even soil depth, can create localized resource pulses that allow some individuals to adopt more competitive or ruderal strategies without affecting the population-level stress tolerance. Similarly, small-scale disturbances, including grazing, trampling, or

periodic soil erosion, can shift resource availability at the individual level, promoting CSR variation within populations. These effects emphasize that, for example, species like *Afrotrilepis pilosa*, intraspecific ecological strategies variation likely reflects individual responses to microsite heterogeneity and disturbance regimes rather than community-level changes or averaged soil conditions.

Life-history traits can also mediate CSR variation by influencing a species' capacity to adapt to heterogeneous conditions. Mating systems, in particular, shape genetic diversity and thus the range of functional strategies available. **Muñoz *et al.* (2016)** demonstrated that competitive species tend to exhibit higher outcrossing rates, promoting greater genetic variability and adaptive potential, whereas stress-tolerant species are more often associated with mixed mating systems that provide reproductive assurance in harsh environments but limit trait divergence.

In the case of this study, *A. pilosa* may maintain greater functional flexibility partly through increased outcrossing potential, facilitating shifts in trait expression across environmental microsites. Conversely, the predominantly stress-tolerant species (*T. minima*, *S. festivus*, *M. indica*) may rely more on mixed mating for persistence, reinforcing trait stability despite variable soil conditions. This reproductive–ecological linkage could be an additional explanation for the weak soil–trait relationships detected in our study.

Overall, these findings align with **Muñoz *et al.* (2016)**, **de Paula *et al.* (2015)**, and **Rafiee *et al.* (2024)**, who highlight that while soil properties can explain ecological strategies at fine scales, their influence may be obscured when environmental variation is limited or when dominant strategies confer broad edaphic tolerance. Without precise microsite-level environmental measurements (e.g., local soil moisture dynamics or depth in rock depressions), intraspecific trait variation may reflect factors other than the averaged soil properties measured by standard methods.

Therefore, understanding intraspecific variation in CSR strategies and predicting species responses in inselbergs requires perhaps combining soil properties, disturbance regimes, and plasticity, which also has direct implications for conservation prioritization.

Contrary to our initial hypothesis, no significant relationships emerged between CSR strategies and the measured soil variables for any of the four species. Many factors could explain this lack of association. First, soil gradients across the sampled inselbergs may have been relatively narrow, limiting the scope for soil-driven trait variation. While inselberg microhabitats (e.g., shallow depressions, rock pools, mat-form surfaces) often exhibit sharp differences in soil depth, nutrient availability, and moisture (**Porembski *et al.*, 2000**; **de Paula *et al.*, 2015**), our sampling approach, collecting soil at the occurrence point of each individual,

may not have captured this fine-scale heterogeneity. Such microsite variability is known to strongly influence plant functional traits but is often underestimated by standard point-based or composite soil sampling (**Grime, 2001; Fridley et al., 2011**). Higher-resolution soil measurements or in situ monitoring of micro-environmental conditions could improve detection of soil-trait links.

Also, 3 (*T. minima*, *S. festivus*, *M. indica*) of the 4 species presented predominantly stress-tolerant strategies, showing strong adaptation to persist under a wide range of edaphic conditions. Similar patterns have been reported for desiccation-tolerant inselberg plants (e.g., *A. pilosa*, Cyperaceae mats), which maintain functional stability across highly variable and nutrient-poor substrates (**Porembski, 2007; Scarano, 2009**).

This ecological buffering could weaken observable soil-trait correlations at the scales examined. While **Rafiee et al. (2024)** showed that soil variables have a stronger effect on species CSR strategies than climate variables, inselberg DT species often maintain trait stability across wide edaphic ranges (e.g., *M. flabellifolia*; **Farrant and Moore, 2011**), with variation emerging more from microclimatic, disturbance, or genetic factors than from averaged soil measures.

This aligns with **de Paula et al. (2015)**, who found that microhabitat heterogeneity, rather than soil variables, largely explains the coexistence of distinct CSR strategies in inselberg communities. For *A. pilosa*, broader functional strategies may confer resistance to environmental fluctuations and disturbances, but also indicate that soil is not the primary driver of intraspecific variation. Effective conservation of DT inselberg species should combine soil conditions, disturbance regimes, and species-specific adaptive capacities rather than focusing on soil variables alone.

Although soil properties showed limited influence on ecological strategies of the studied DT species, other factors may still contribute to variation in desiccation tolerance. Factors such as seed age are particularly relevant under increasing drought conditions. The moderate but consistent negative trend in SPEI values over time indicates that both *M. indica* and *T. minima* will experience more drought due to climate change, supporting our first hypothesis (i.e., that climate change is increasing species exposure to drought).

Our second hypothesis (i.e., that seed age will affect the desiccation tolerance capacity of seedlings at different developmental stages) was only partially confirmed. For both species, seedlings from older seeds have a lower capacity to cope with desiccation in stage 1 of their development. This might indicate that both species might be found vulnerable to drought events that occur shortly after the germination of their older seeds. Moreover, *M. indica* might be more



vulnerable than *T. minima*, once seedlings from older seeds of this species show a lower recovery from desiccation in stage 7 (after no difference in desiccation tolerance due to different seed age between stages 2 and 6).

Species are not only being more exposed to droughts due to climate change, but they are also experiencing more consecutive months with abnormal droughts (i.e., SPEI values lower than -1). This might indicate that climate change is causing droughts to be more severe and last longer in the localities where species occur. This trend, combined with the fact that both species are associated with inselbergs, could significantly affect the success of seedlings' establishment.

Inselbergs are rock outcrops characterized by habitats with low soil, and consequently low soil moisture retention (**Porembski, 2000; Burke, 2003; Porembski, 2007**). In inselbergs, seeds of these species might often rely on a narrower window of favorable moisture conditions to germinate and grow in earlier stages of their development. If such windows of favorable moisture conditions are delayed and shortened, the mortality within both species due to drought is likely to increase because there would be more seedlings from older seeds experiencing desiccation tolerance shortly after germination (and seed age is associated with a lower desiccation tolerance ability in stage 1 of their seedling development).

For example, a one-week moisture period within an abnormally dry period can be enough to trigger germination, but not for continued growth, exposing seedlings to desiccation shortly after their germination. In *Tripogon minima*, germination begins within three days of moisture availability, with 6% of seeds reaching stage 2 by Day 3 while the majority (94%) remain in stage 1. By Day 5, seedlings show rapid early development, with noticeable shifts into stages 3 (10%), 4 (13%), and 5 (4%), although advanced stages (6-7) are still absent. By Day 7, more than half of the population (56%) remains in stage 1, while an important proportion has progressed to stages 4 (20%), 5 (17%), and 6 (2%), with stage 7 still having 0%. From Day 15, advanced stages become dominant (stage 6: 31%), and stage 1 declines to below 10%, with stage 7 reaching 9%.

This progression indicates that although brief wet periods (3-4 days) can rapidly initiate germination, advancement to more desiccation-resistant developmental stages requires sustained moisture for one to two weeks. In other words, germination occurs quickly, but the transition to later developmental stages is considerably slower, leaving seedlings at high risk of mortality if drought occurs too soon.

The importance of continued favorable moisture conditions is more special for *T. minima*. The results show a variation in desiccation tolerance across developmental stages, even in younger seeds. Between stages 2 and 6, survival was 100% but dropped below 90% at stages 1 and 7,

regardless of seed age. Although the desiccation tolerance was high across all the stages, these results indicate that the seedlings of this species are more sensitive to drought in those specific stages. Thus, drought during the first 48 hours after moisture availability or again around two weeks later, when seedlings reach full development, results in the greatest mortality. For this species, it is therefore critical that the onset of the rainy season is followed by at least two weeks of continuous moisture without early drying, to allow seedlings to safely pass through these vulnerable stages.

If future droughts delay germination, it would increase seed aging in the seed bank, increasing their exposure to aging processes that can negatively affect their viability. Earlier studies have shown that seed age affects seed viability, reducing germination rate (**Soltani *et al.*, 2008**), meaning fewer seeds successfully sprout after extended dormancy. In addition, older seeds often produce seedlings with reduced vigor and growth potential, which can impair early development and survival (**Joaoabba and Lovato, 1999**). This decline in seedling performance can further limit successful developmental stages in the field. Moreover, aging may affect the ability of seedlings to progress through critical developmental stages (**Verma *et al.*, 2003**). Collectively, these effects reduce the likelihood of seeds' effective contribution to population regeneration, posing a risk for long-term species persistence, especially under changing climate conditions that extend dry periods.

Another problem species might face due to increasing exposure to drought is whether favorable moisture conditions would allow plants to reach their reproductive stages. Even though germination timing adjusts to new rainfall patterns, plants might experience droughts that would stop their development and reduce their reproductive output. Lower seed production diminishes inputs to the soil seed bank, potentially compromising long-term population persistence. Annual species such as *Microchloa indica* may be particularly vulnerable, as they rely on completing their entire life cycle within a single season and cannot survive across years through vegetative structures.

For these species, a failed reproductive event means the complete loss of that year's contribution to the seed bank. Additionally, altered rainfall patterns and uneven developmental rates among populations could disrupt the synchrony of flowering, reducing opportunities for cross-pollination and further lowering seed set. Together, these factors could weaken population, erode genetic diversity, and accelerate declines in species dependent on tightly timed life cycles in seasonal environments.

Thus, dormancy may emerge as a strategy allowing seeds to delay germination until more favorable conditions return, helping to avoid short or anticipated rainfall events. Although

dormancy has been widely recognized as an adaptive mechanism to escape drought (**Rees and Long, 1993; Gutterman, 2002; Baskin and Baskin, 2004; Valleriani *et al.*, 2006; Donohue *et al.*, 2010**), some trade-offs are involved.

By prolonging seed age, dormancy can reduce germination rates and seedlings' desiccation tolerance, and it carries physiological costs: metabolic integrity may decline through gradual depletion of energy reserves, accumulation of oxidative damage, and loss of membrane stability. These age-related changes can impair stress tolerance, slow early growth, and ultimately reduce the contribution of aged seeds to recruitment. While dormancy may prevent immediate mortality under drought, it can also limit the long-term regenerative potential of the seed bank, particularly if extended dry periods become more frequent under future climate scenarios.

Plants are therefore vulnerable to climate change if the costs of dormancy outweigh its benefits. Moreover, desiccation tolerance itself may be modulated by environmental conditions such as desiccation rate (**Farrant and Kruger, 2001; Marks *et al.*, 2021**). Therefore, the assumption that DT plants are “safe” under future climates because they might resist extreme conditions is misleading: while they may be physiologically capable of surviving drought, this does not necessarily guarantee successful development, as conditions may exceed their capacity to withstand stress, whether during early developmental stages or later in adulthood.

It must also be good to take into account factors such as the legacy effects of drought (e.g., alterations in carbon and nitrogen cycling, plant growth and phenology, plant resilience/recovery, species composition, and soil properties; **Vilonen *et al.*, 2022**) or stress memory (e.g., the proposed ability of *Myrothamnus flabellifolius* to record previous drought events and activate protective responses more rapidly and effectively during subsequent stresses, thereby mitigating the negative effects of drought; **Bentley and Farrant, 2020**). They can hamper the understanding of drought impact on species and highlight the importance of investigating these processes in greater detail.

Future research should perhaps integrate physiological, ecological, and climatic perspectives to assess how factors such as seed aging, developmental stage vulnerability, reproductive failure, habitat-specific constraints, and drought-related factors affect species persistence. Such approach is essential for refining predictions of plant responses under future climate scenarios and for developing conservation strategies that address both immediate and long-term challenges posed by increasingly severe and prolonged droughts.

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## **CONCLUSION**

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Understanding the composition, distribution, and ecological drivers of plant groups within a region is essential for assessing biodiversity patterns and guiding effective conservation strategies. In this context, desiccation-tolerant (DT) vascular plants represent a unique yet understudied component of West African flora, whose ecological roles and environmental sensitivities remain poorly documented.

This thesis investigated the factors controlling the distribution of desiccation-tolerant (DT) vascular plants in West Africa, with a focus on understanding how climatic, edaphic and biological drivers shape their current and potential distributions under changing environmental conditions. Although DT plants can withstand extreme dehydration, the mechanisms determining their spatial distribution and their responses to anthropogenic pressures remain poorly documented. This study addressed this knowledge gap by integrating biogeographical, ecological and physiological approaches to identify the main determinants influencing the occurrence, diversity and persistence of DT plants in West Africa. Through four complementary objectives, this work revealed that both environmental and anthropogenic factors jointly control the distribution and vulnerability of DT species in the region.

The first objective was to evaluate the current state of knowledge and conservation status of DT plants in West Africa. This study produced the region's first comprehensive inventory of DT vascular plant species, revealing 49 species distributed across multiple countries, a taxonomically and ecologically diverse group, yet it remains largely neglected in conservation assessments. Only 14% of the identified species have been evaluated by the IUCN, and only a small fraction of studies explicitly address their conservation needs. Furthermore, those few studies often did so without providing sufficient quantitative evidence to justify conservation prioritization. This knowledge gap is particularly concerning given that the analysis of species exposure showed that the two species with the lowest protection levels are also found to be the most exposed to quarrying and climate change, highlighting an uneven distribution of conservation efforts and a potential mismatch between species vulnerability and protection coverage, showing a strong bias in the current protected area network. While protected areas may effectively reduce quarrying pressure on inselbergs, they are unlikely to mitigate the negative effects of climate change. These findings demonstrate that the distribution of DT plants is not solely controlled by their physiological desiccation-tolerance, but also by socio-environmental factors, including habitat disturbance and inadequate conservation representation.

The second objective examined how climatic variables influence (impacts of climate change) both species' distribution and diversity patterns of DT species. The projection has shown a consistent contraction of species distribution ranges and habitat fragmentation, which might unfold a reduced carrying capacity, rescue effect and local extinction due to climatic factors, particularly precipitation seasonality and temperature extremes, which in this study are found to be the key drivers of DT plant occurrence across West Africa. On one hand, suitable areas for most DT species are expected to contract significantly, with a marked decline in both the extent and connectivity of suitable areas. On one another, the results show a significant shrinkage of both centers of diversity and endemism, threatening the diversity of DT plants in West Africa, from southern Cameroon to continental Equatorial Guinea and along the coastal corridor from Senegal to Cameroon, suggesting that climate change will become a dominant factor limiting the future distribution of DT species, and that without adaptive conservation measures, many DT species may lose large portions of their potential habitats by the end of the century, despite their intrinsic desiccation tolerance.

The third objective investigated the role of soil in influencing intraspecific variation in species' ecological strategies, with the hypothesis that soil characteristics significantly contribute to shifts in ecological strategies within species. Contrary to expectations, there is no relationship detected between measured soil variables and CSR strategies for any of the four desiccation-tolerant grasses. Although no significant relationships were found, these findings contribute to the growing recognition that the drivers of intraspecific variation in plant ecological strategies could be complex and context-dependent and may be synergetic for them to influence CSR strategies. The observed predominance of stress-tolerant strategies in three species may indicate an overriding influence of disturbance-related stressors over soil resource variation.

While the fourth objective highlights that certain DT plant species are likely to face increasing challenges under future climate scenarios, not only because of greater drought frequency and severity, but also due to the effects of seed age and developmental stage-specific desiccation sensitivity. The experiments conducted on *Microchloa indica* and *Tripogonella minima* revealed that increasing drought frequency and intensity, coupled with seed age and developmental stage, could compromise desiccation tolerance by influencing desiccation recovery and regeneration success under future climates, as older seeds have reduced tolerance. These results underscore that the persistence of DT species is not only determined by adult physiological traits but also by early life-stage dynamics and seed physiology. This developmental sensitivity may represent a critical factor limiting population regeneration under

increasing drought frequency and intensity predicted for the region. While desiccation tolerance and dormancy confer advantages, their benefits can be offset by physiological costs and environmental limitations, particularly when droughts occur at vulnerable life stages. Moreover, legacy effects of drought and stress memory may further complicate predictions of species' responses.

This thesis provides a comprehensive and integrative assessment of the factors shaping the distribution of desiccation-tolerant plants in West Africa. By combining biogeographic, physiological and functional approaches, it reveals that although DT plants are resistant to severe drought, their persistence is increasingly threatened by climatic instability, habitat disturbance and limited conservation attention. These findings show that desiccation tolerance does not equate to invulnerability and that the survival of DT species will depend on coordinated conservation, research and policy actions that address the multiple dimensions of global environmental change.

## **Perspectives**

The findings of this thesis provide promising perspectives for future research on DT vascular plants. First, the framework developed, combined distribution modeling, trait-based analysis and physiological experimentation, that could serve as a foundation for multiscale studies by linking individual physiological responses to community- and landscape-level processes. Particularly, the predictive models and trait datasets generated could be expanded to incorporate genetic, phylogenetic and functional diversity, allowing a deeper understanding of the evolutionary and ecological dimensions of desiccation tolerance.

In addition, the low proportion of desiccation-tolerant plants assessed by the IUCN highlights a major gap in current conservation knowledge. Future research could further explore the integration of these species into national and regional Red Lists, in order to improve understanding of their conservation status and ecological importance.

Second, the results stress the need to monitor DT plant species as well as their habitats in the long term, taking into account the fact that inselbergs, which serve as refugia for DT plants, remain among the least-studied ecosystems in West Africa. Therefore, establishing standardized monitoring networks across representative inselbergs in West Africa would allow researchers to quantify temporal changes in species diversity, microclimatic conditions and disturbance pressures. Such kind of efforts would improve the prediction of species persistence and inform adaptive management.

Third, it could be beneficial if future researches could explore mechanistic approaches to better understand the physiological, genetic and ecological trade-offs associated with desiccation tolerance. Hence, integrating experimental ecology, ecophysiology and genomics would help to clarify how DT plants balance tolerance, growth and reproduction under fluctuating environmental conditions, and also identify functional thresholds beyond which those species tolerance mechanisms fail under future climate extremes.

Furthermore, advancing our understanding of desiccation-tolerant plants requires integrating multiple scales of analysis, from local population processes to landscape-level patterns. At the population scale, exploring fine-scale variability among individuals is crucial to uncover the mechanisms underlying desiccation tolerance. Combining microclimatic monitoring, soil microbiome analyses and assessments of phenotypic plasticity would help reveal how local environmental gradients shape species' ecological strategies and adaptive potential. At broader spatial scales, investigating climate-soil-trait interactions across heterogeneous landscapes can provide insights into the environmental factors controlling DT species' distribution and persistence. The integration of remote sensing tools, microclimatic sensors and high-resolution soil mapping, combined with targeted fieldwork, would capture micro-environmental heterogeneity and improve predictive models of species' responses to climate change.

Exploring life-stage vulnerabilities and stress memory mechanisms under both experimental and field (natural) conditions will be crucial to assess the capacity of DT species to persist under increasingly frequent and severe droughts.

Finally, escalating the geographical scope of DT plant research beyond West Africa to include comparative studies across sub-Saharan Africa and other tropical regions (e.g., Madagascar, Central Africa, South Africa, Brazil's *campos rupestres*) would help to refine biogeographic patterns, to identify potential refugia and to detect convergent adaptive strategies. Also, integrating broader field surveys with molecular and physiological approaches would further clarify the genetic basis and variability of desiccation tolerance, ultimately contributing to a global framework for understanding how DT plants respond to climate change and land-use transformation.

## **Recommendations**

Some recommendations can be made based on the findings of this study to guide conservation, research and policy actions regarding desiccation-tolerant vascular plants.



### **1. Integrate desiccation-tolerant plants and inselberg ecosystems into conservation planning**

Inselbergs and other rock outcrops should be explicitly recognized as priority habitats in biodiversity conservation strategies. Protected area networks must be expanded or adjusted to ensure adequate representation of these ecosystems. Management plans should also address localized anthropogenic pressures, such as quarrying and land conversion, which are currently the main threats to desiccation-tolerant plants and promote site-specific protection and sustainable land-use practices in order to maintain their ecological integrity.

### **2. Incorporate climate projections into the management of desiccation-tolerant plants**

Conservation planning must explicitly account for the anticipated range contractions, fragmentation and suitable area shifts of desiccation-tolerant plants under climate change. The use of species distribution models and climate-envelope analyses should be considered to guide the identification of potential refugia and future conservation priorities. Also, protected areas and adaptive management frameworks must be established to respond with dynamism to changing environmental conditions. This is particularly urgent, as the results indicate that despite the importance of protected areas, while the latter can mitigate quarrying, they offer limited buffering against climate-driven impacts.

### **3. Promote integrative and interdisciplinary research.**

A collaboration between ecologists, physiologists, soil scientists and geneticists could be essential to build a mechanistic understanding of DT plant ecology. Therefore, thinking about cross-disciplinary projects could be a good idea to investigate the physiological, ecological and evolutionary dimensions of DT plants taking into account functional genomics, phenotype plasticity, and climate models to advance predictions of population responses under combined stress scenarios and identify thresholds beyond which tolerance mechanisms might fail.

### **4. Foster capacity building and regional collaboration.**

Strengthen local research capacity is essential for the long-term conservation of DT plants in West Africa, this could be achieved by investing in training programmes, local herbarium digitization, and regional data-sharing platforms. Such initiatives will ensure that conservation planners and decision-makers are informed by the most recent scientific evidence and locally grounded expertise.

## **5. Develop targeted conservation strategies for desiccation-tolerant plants**

A flexible management approaches should be developed to safeguard DT plants, particularly those with restricted ranges. When direct interventions are not feasible, the use of umbrella or surrogate species can provide indirect protection, and ex-situ conservation efforts (seed banks, botanical gardens etc.) could be used and should prioritized for the most threatened species to ensure genetic preservation and potential restoration opportunities, in case it is possible.

## **6. Explore applied implications for agriculture and ecosystem restoration**

Considering many previous studies, the physiological mechanisms of DT plants offer promising opportunities for applied innovation. Therefore, insights into their stress tolerance and recovery pathways could inform the development of drought-resistant crops or guide restoration strategies in certain degraded drylands. Bridging ecological research with applied sciences would contribute to sustainable land management and climate adaptation efforts across sub-Saharan Africa.

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## **APPENDICIES**

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## Appendix 1

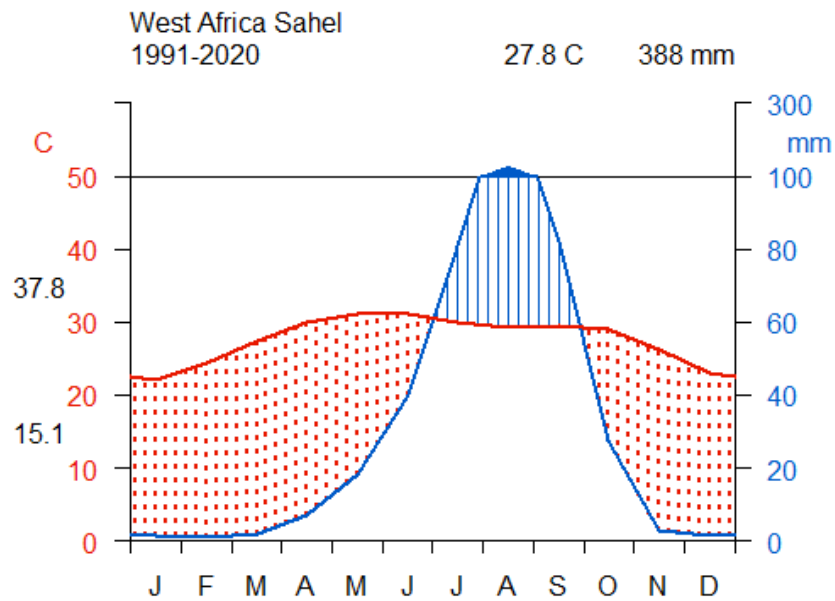


Figure A 1: Ombrothermic curve of Sahelian zone (West Africa)

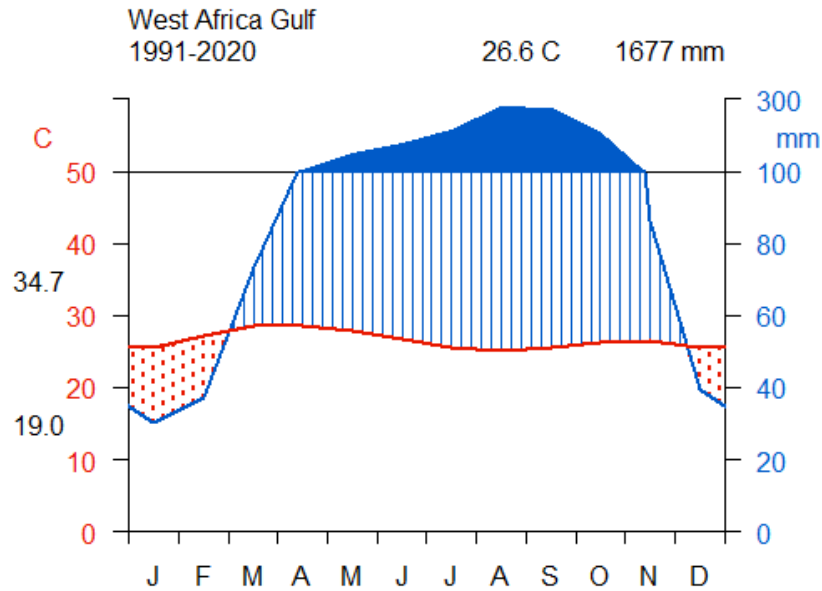


Figure A 2: Ombrothermic curve of the Humid zone (Gulf, West Africa)

## Appendix 2

**Table A1:** Reference of occurrence datasets retrieved from GBIF database.

| Species                             | GBIF (references)                                                                                                                           |
|-------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Actiniopteris radiata</i>        | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.w7xj3c">https://doi.org/10.15468/dl.w7xj3c</a>    |
| <i>Actiniopteris semiflabellata</i> | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.u46p8v">https://doi.org/10.15468/dl.u46p8v</a>    |
| <i>Adiantum incisum</i>             | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.m4pmmc">https://doi.org/10.15468/dl.m4pmmc</a>    |
| <i>Afrotrilepis jaegeri</i>         | GBIF.org (28 May 2025) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.7nukjh">https://doi.org/10.15468/dl.7nukjh</a>      |
| <i>Afrotrilepis pilosa</i>          | GBIF.org (18 February 2024) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.vmqcx8">https://doi.org/10.15468/dl.vmqcx8</a> |
| <i>Allosorus coriacea</i>           | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.5sremd">https://doi.org/10.15468/dl.5sremd</a>    |
| <i>Arthropteris orientalis</i>      | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.yfu9nx">https://doi.org/10.15468/dl.yfu9nx</a>    |
| <i>Asplenium aethiopicum</i>        | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.hjqzcy">https://doi.org/10.15468/dl.hjqzcy</a>    |
| <i>Asplenium friesiorum</i>         | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.gen6n3">https://doi.org/10.15468/dl.gen6n3</a>    |
| <i>Asplenium megalura</i>           | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.uweaw5">https://doi.org/10.15468/dl.uweaw5</a>    |
| <i>Asplenium monanthes</i>          | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.6c9ztx">https://doi.org/10.15468/dl.6c9ztx</a>    |
| <i>Asplenium sandersonii</i>        | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.k5hvx2">https://doi.org/10.15468/dl.k5hvx2</a>    |
| <i>Asplenium stuhlmannii</i>        | GBIF.org (18 February 2024) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.2bncdt">https://doi.org/10.15468/dl.2bncdt</a> |
| <i>Cheilanthes inaequalis</i>       | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.xba4pw">https://doi.org/10.15468/dl.xba4pw</a>    |
| <i>Coleochloa abyssinica</i>        | GBIF.org (28 May 2025) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.j3xsse">https://doi.org/10.15468/dl.j3xsse</a>      |
| <i>Coleochloa domensis</i>          | GBIF.org (28 May 2025) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.32hthf">https://doi.org/10.15468/dl.32hthf</a>      |
| <i>Cosentinia vellea</i>            | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.dafh4z">https://doi.org/10.15468/dl.dafh4z</a>    |
| <i>Craterostigma plantagineum</i>   | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.pnxv3a">https://doi.org/10.15468/dl.pnxv3a</a>    |
| <i>Craterostigma yaundense</i>      | GBIF.org (18 February 2024) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.huy7m8">https://doi.org/10.15468/dl.huy7m8</a> |
| <i>Crepidomanes chevalieri</i>      | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.we3am5">https://doi.org/10.15468/dl.we3am5</a>    |



|                                     |                                                                                                                                             |
|-------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Crepidomanes melanotrichum</i>   | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.r2sdq5">https://doi.org/10.15468/dl.r2sdq5</a>    |
| <i>Didymoglossum erosum</i>         | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.9avcdb">https://doi.org/10.15468/dl.9avcdb</a>    |
| <i>Elaphoglossum acrostichoides</i> | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.698qkw">https://doi.org/10.15468/dl.698qkw</a>    |
| <i>Heminiotis farinosa</i>          | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.vzzhtk">https://doi.org/10.15468/dl.vzzhtk</a>    |
| <i>Hymenophyllum capillare</i>      | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.wqpewp">https://doi.org/10.15468/dl.wqpewp</a>    |
| <i>Hymenophyllum hirsutum</i>       | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.rr3cxv">https://doi.org/10.15468/dl.rr3cxv</a>    |
| <i>Hymenophyllum kuhnii</i>         | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.f529nm">https://doi.org/10.15468/dl.f529nm</a>    |
| <i>Hymenophyllum splendidum</i>     | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.7j4fhq">https://doi.org/10.15468/dl.7j4fhq</a>    |
| <i>Loxogramme abyssinica</i>        | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.tdve7b">https://doi.org/10.15468/dl.tdve7b</a>    |
| <i>Melpomene flabelliformis</i>     | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.82wkxt">https://doi.org/10.15468/dl.82wkxt</a>    |
| <i>Microchloa indica</i>            | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.4pek7h">https://doi.org/10.15468/dl.4pek7h</a>    |
| <i>Microchloa kunthii</i>           | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.sym7kq">https://doi.org/10.15468/dl.sym7kq</a>    |
| <i>Microdracoides squamosa</i>      | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.6pwvgd">https://doi.org/10.15468/dl.6pwvgd</a>    |
| <i>Oropetium aristatum</i>          | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.uuvqb7">https://doi.org/10.15468/dl.uuvqb7</a>    |
| <i>Oropetium capense</i>            | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.r6247a">https://doi.org/10.15468/dl.r6247a</a>    |
| <i>Pellaea dura</i>                 | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.zsgpw2">https://doi.org/10.15468/dl.zsgpw2</a>    |
| <i>Phymatosorus scolopendria</i>    | GBIF.org (18 February 2024) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.vk237u">https://doi.org/10.15468/dl.vk237u</a> |
| <i>Platycterium stemaria</i>        | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.ffzdam">https://doi.org/10.15468/dl.ffzdam</a>    |
| <i>Pleopeltis macrocarpa</i>        | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.ekk9fu">https://doi.org/10.15468/dl.ekk9fu</a>    |
| <i>Polyphlebium borbonicum</i>      | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.zvdfg9">https://doi.org/10.15468/dl.zvdfg9</a>    |

|                                  |                                                                                                                                             |
|----------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Selaginella njamnjamensis</i> | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.5uud4g">https://doi.org/10.15468/dl.5uud4g</a>    |
| <i>Sporobolus festivus</i>       | GBIF.org (18 February 2024) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.m8h3dp">https://doi.org/10.15468/dl.m8h3dp</a> |
| <i>Sporobolus pellucidus</i>     | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.7khsy2">https://doi.org/10.15468/dl.7khsy2</a>    |
| <i>Sporobolus stapfianus</i>     | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.nx4pse">https://doi.org/10.15468/dl.nx4pse</a>    |
| <i>Tripogon major</i>            | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.pmnuqm">https://doi.org/10.15468/dl.pmnuqm</a>    |
| <i>Tripogon multiflorus</i>      | GBIF.org (28 May 2025) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.9m6dnc">https://doi.org/10.15468/dl.9m6dnc</a>      |
| <i>Tripogonella minima</i>       | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.gzfvm3">https://doi.org/10.15468/dl.gzfvm3</a>    |
| <i>Vittaria guineensis</i>       | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.8ng3dd">https://doi.org/10.15468/dl.8ng3dd</a>    |
| <i>Xerophyta schnizleinia</i>    | GBIF.org (22 March 2023) GBIF Occurrence Download<br><a href="https://doi.org/10.15468/dl.suyyug">https://doi.org/10.15468/dl.suyyug</a>    |

**Table A2:** Bioclimatic variables retrieved from CHELSA database and used in this study.

| Bioclimatic variables                                               |
|---------------------------------------------------------------------|
| - BIO1 – Annual Mean Temperature                                    |
| - BIO2 – Mean Diurnal Range (Mean of monthly (max temp - min temp)) |
| - BIO3 – Isothermality (BIO2/BIO7) (×100)                           |
| - BIO4 – Temperature Seasonality (standard deviation ×100)          |
| - BIO5 – Max Temperature of Warmest Month                           |
| - BIO7 – Temperature Annual Range (BIO5-BIO6)                       |
| - BIO8 – Mean Temperature of Wettest Quarter                        |
| - BIO12 – Annual Precipitation                                      |
| - BIO13 – Precipitation of Wettest Month                            |
| - BIO14 – Precipitation of Driest Month                             |
| - BIO15 – Precipitation Seasonality (Coefficient of Variation)      |
| - BIO16 – Precipitation of Wettest Quarter                          |
| - BIO17 – Precipitation of Driest Quarter                           |
| - BIO18 – Precipitation of Warmest Quarter                          |
| - BIO19 – Precipitation of Coldest Quarter                          |

**Table A3:** List of R packages used in this study.

| Packages | References |
|----------|------------|
|----------|------------|

|               |                                                                                                                                                                                                                                                                  |
|---------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| dplyr         | Wickham H, François R, Henry L, Müller K, Vaughan D (2023). dplyr: A Grammar of Data Manipulation. R package version 1.1.4, <a href="https://CRAN.R-project.org/package=dplyr">https://CRAN.R-project.org/package=dplyr</a>                                      |
| forcats       | Wickham H (2023). forcats: Tools for Working with Categorical Variables (Factors). R package version 1.0.0, <a href="https://CRAN.R-project.org/package=forcats">https://CRAN.R-project.org/package=forcats</a>                                                  |
| ggplot2       | Wickham H (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. R package version 3.5.0, <a href="https://CRAN.R-project.org/package=ggplot2">https://CRAN.R-project.org/package=ggplot2</a>                                            |
| ggpubr        | Kassambara A (2023). ggpubr: 'ggplot2' Based Publication Ready Plots. R package version 0.6.0, <a href="https://CRAN.R-project.org/package=ggpubr">https://CRAN.R-project.org/package=ggpubr</a>                                                                 |
| mapdata       | Brownrigg R, Minka TP, Deckmyn A (2023). mapdata: Extra Map Databases. R package version 2.3.1, <a href="https://CRAN.R-project.org/package=mapdata">https://CRAN.R-project.org/package=mapdata</a>                                                              |
| maps          | Becker RA, Wilks AR, Brownrigg R, Minka TP, Deckmyn A (2023). maps: Draw Geographical Maps. R package version 3.4.1, <a href="https://CRAN.R-project.org/package=maps">https://CRAN.R-project.org/package=maps</a>                                               |
| phytools      | Revell LJ (2012). phytools: An R package for phylogenetic comparative biology (and other things). <i>Methods in Ecology and Evolution</i> , 3(2), 217–223. <a href="https://CRAN.R-project.org/package=phytools">https://CRAN.R-project.org/package=phytools</a> |
| rnaturalearth | South A (2017). rnaturalearth: World Map Data from Natural Earth. R package version 0.1.0, <a href="https://CRAN.R-project.org/package=rnaturalearth">https://CRAN.R-project.org/package=rnaturalearth</a>                                                       |
| sf            | Pebesma E (2018). Simple Features for R: Standardized Support for Spatial Vector Data. <i>R Journal</i> , 10(1), 439–446. <a href="https://CRAN.R-project.org/package=sf">https://CRAN.R-project.org/package=sf</a>                                              |
| terra         | Hijmans R (2023). terra: Spatial Data Analysis. R package version 1.7-65, < <a href="https://CRAN.R-project.org/package=terra">https://CRAN.R-project.org/package=terra</a> >                                                                                    |
| V.PhyloMaker  | Jin, Y & Qian, H. 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. <i>Ecography</i> . 42(8):1353–1359. <a href="https://doi.org/10.1111/ecog.04434">doi.org/10.1111/ecog.04434</a>                                 |
| viridis       | Garnier S (2021). viridis: Default Color Maps from 'matplotlib'. R package version 0.6.4, <a href="https://CRAN.R-project.org/package=viridis">https://CRAN.R-project.org/package=viridis</a>                                                                    |
| waffle        | Rudis B, Gandy D 2023. waffle: Create Waffle Chart Visualizations. R package version 1.0.2, <a href="https://CRAN.R-project.org/package=waffle">https://CRAN.R-project.org/package=waffle</a>                                                                    |

**Table A4:** Studies about desiccation-tolerant vascular plants in West Africa. Q1 - Did the study discuss conservation needs of DT plants?; Q2 - Did the study provide enough evidence that justifies the conservation needs of DT plants?; Q3 - Did the study propose effective conservation strategies for DT plants?; Categories: I - Studies focusing on the entire

community; II - studies focusing on specific community components; III - studies focusing on ecological processes and functioning.

| References                                                                                                                                                                                                                                                      | Q1  | Q2 | Q3 | Categories |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|----|----|------------|
| Gaff, D. F. (1986). Desiccation tolerant 'resurrection'grasses from Kenya and West Africa. <i>Oecologia</i> , 70, 118-120.                                                                                                                                      | No  | No | No | II         |
| Krieger, A., Porembski, S., & Barthlott, W. (2000). Vegetation of seasonal rock pools on inselbergs situated in the savanna zone of the Ivory Coast (West Africa). <i>Flora</i> , 195(3), 257-266.                                                              | No  | No | No | II         |
| Müller, J. V. (2007). Herbaceous vegetation of seasonally wet habitats on inselbergs and lateritic crusts in West and Central Africa. <i>Folia Geobotanica</i> , 42, 29-61.                                                                                     | No  | No | No | II         |
| Oumorou, M., & Lejoly, J. (2003). Écologie, flore et végétation de l'inselberg Sobakperou (Nord-Bénin). <i>Acta botanica gallica</i> , 150(1), 65-84.                                                                                                           | No  | No | No | I          |
| Owoseye, J. A., & Sanford, W. W. (1972). An ecological study of <i>Vellozia schnitzleinia</i> , a drought-enduring plant of northern Nigeria. <i>The Journal of Ecology</i> , 807-817.                                                                          | No  | No | No | II         |
| Parmentier, I. (2001). Premières études sur la diversité végétale des inselbergs de Guinée Équatoriale continentale. <i>Systematics and Geography of Plants</i> , 911-922.                                                                                      | No  | No | No | I          |
| Parmentier, I., & Hardy, O. J. (2009). The impact of ecological differentiation and dispersal limitation on species turnover and phylogenetic structure of inselberg's plant communities. <i>Ecography</i> , 32(4), 613-622.                                    | No  | No | No | I          |
| Parmentier, I., Oumorou, M., Pauwels, L., & Lejoly, J. (2006). Comparison of the ecology and distribution of the Poaceae flora on inselbergs embedded in savannah (Benin) or in rain forest (Western Central Africa). <i>Belgian Journal of Botany</i> , 65-77. | No  | No | No | II         |
| Porembski, S. (2000). The invasibility of tropical granite outcrops ('inselbergs') by exotic weeds. <i>Journal of the Royal society of Western Australia</i> , 83, 131.                                                                                         | Yes | No | No | III        |

|                                                                                                                                                                                                                                                                      |     |    |    |     |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|----|----|-----|
| Porembski, S. (2007). Tropical inselbergs: habitat types, adaptive strategies and diversity patterns. <i>Brazilian Journal of Botany</i> , 30, 579-586.                                                                                                              | Yes | No | No | I   |
| Porembski, S., & Barthlott, W. (1996). Plant species diversity of West African inselbergs. In <i>The Biodiversity of African Plants: Proceedings XIVth AETFAT Congress 22–27 August 1994, Wageningen, The Netherlands</i> (pp. 180-187). Springer Netherlands.       | No  | No | No | I   |
| Porembski, S., & Barthlott, W. (1997). Seasonal Dynamics of Plant Diversity on Inselbergs in the Ivory Coast (West Africa). <i>Botanica Acta</i> , 110(6), 466-472.                                                                                                  | No  | No | No | I   |
| Porembski, S., & Watve, A. (2005). Remarks on the species composition of ephemeral flush communities on paleotropical rock outcrops. <i>Phytocoenologia</i> , 389-402.                                                                                               | No  | No | No | II  |
| Porembski, S., Barthlott, W., Dörrstock, S., & Biedinger, N. (1994). Vegetation of rock outcrops in Guinea: granite inselbergs, sandstone table mountains and ferricretes—remarks on species numbers and endemism. <i>Flora</i> , 189(4), 315-326.                   | Yes | No | No | I   |
| Porembski, S., Becker, U., & Seine, R. (2000). Islands on islands: habitats on inselbergs. In <i>Inselbergs: biotic diversity of isolated rock outcrops in tropical and temperate regions</i> (pp. 49-67). Berlin, Heidelberg: Springer Berlin Heidelberg.           | No  | No | No | II  |
| Porembski, S., Brown, G., & Barthlott, W. (1996). A species-poor tropical sedge community: <i>Afrotrilepis pilosa</i> mats on inselbergs in West Africa. <i>Nordic Journal of Botany</i> , 16(3), 239-245.                                                           | No  | No | No | II  |
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|                                                                                                                                                                      |    |    |    |   |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|
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|---------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|----|
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|                                                                                                                                                                                                                                               |    |    |    |   |
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|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|

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|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|
| Tindano, E., Ganaba, S., Sambare, O., & Thiombiano, A. (2015). Sahelian inselberg vegetation in Burkina Faso. <i>Bois &amp; Forêts des Tropiques</i> , 325(3), 21–33. | No | No | No | I |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|

|                                                                                                                                              |    |    |    |   |
|----------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|
| Tindano, E., Kaboré, G. E., Porembski, S., & Thiombiano, A. (2024). Plant communities on inselbergs in Burkina Faso. <i>Heliyon</i> , 10(1). | No | No | No | I |
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|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|
| Tindano, E., Kadéba, A., Traoré, I. C. E., & Thiombiano, A. (2023). Effects of abiotic factors on the flora and vegetation of inselbergs in Burkina Faso. <i>Environmental Advances</i> , 12, 100378. | No | No | No | I |
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|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|
| Tindano, E., Lankoandé, B., Porembski, S., & Thiombiano, A. (2023). Inselbergs: potential conservation areas for plant diversity in the face of anthropization. <i>J. Phytol</i> , 15, 70-79. | No | No | No | I |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|

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|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|
| Tindano, E., Porembski, S., Koehler, J., & Thiombiano, A. (2021). Ecological and floristic characterization of inselberg habitats in Burkina Faso. <i>Geo-Eco-Trop</i> , 45(4), 573-588. | No | No | No | I |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|---|

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**Table A5:** Species presence (1) and absence (0) across 123 inselbergs in West Africa. Ap – *Afrotrilepis pilosa*, As - *Asplenium stuhlmannii*, Cy - *Craterostigma yaundense*, Mi - *Microchloa indica*, Ms - *Microdracoides squamosa*, Oa - *Oropetium aristatum*, Pd - *Pellaea doniana*, Ps - *Phymathosorus scolopendria*, Sf - *Sporobolus festivus*, Tm - *Tripogonella minima*.

| Inselbergs                  | Longitude | Latitude | Ap | As | Cy | Mi | Ms | Oa | Pd | Ps | Sf | Tm |
|-----------------------------|-----------|----------|----|----|----|----|----|----|----|----|----|----|
| Mt. Niangbo                 | -5.1775   | 8.8275   | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Mt. Korhogo                 | -5.650833 | 9.4525   | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Nambelegue                  | -5.675833 | 9.473889 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Near Korhogo                | -5.615556 | 9.501111 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Boundiali 1                 | -6.494444 | 9.534167 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Boundiali 2                 | -6.626111 | 9.596667 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Boundiali 3                 | -6.488056 | 9.493889 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Séguéla 1                   | -6.544722 | 7.900278 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Séguéla 2                   | -6.533333 | 7.9075   | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Séguéla (road to Mankono) 1 | -6.638056 | 8.037222 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Séguéla (road to Mankono) 2 | -6.640556 | 8.029444 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 0  |
| Man (Cascade)               | -7.628056 | 7.494722 | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  |
| Danané                      | -8.131667 | 7.269444 | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  |
| Duékoué 1                   | -7.365556 | 6.756389 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 0  |
| Duékoué 2                   | -7.376111 | 6.751111 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 0  |
| Man (Dent de Man)           | -7.541667 | 7.452222 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 0  |
| Mt. Niénokoué               | -7.17     | 5.434444 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |
| Rocher d'Issia              | -6.581111 | 6.483333 | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 0  |
| Dabakala (Kadjeoule-Sourdi) | -4.546667 | 8.419444 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Nassian (Gbonkonou)         | -3.500278 | 8.45     | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  |
| Man (Cissus)                | -7.575833 | 7.424167 | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 1  | 0  |
| Tai-National Park           | -7.209722 | 5.4625   | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |

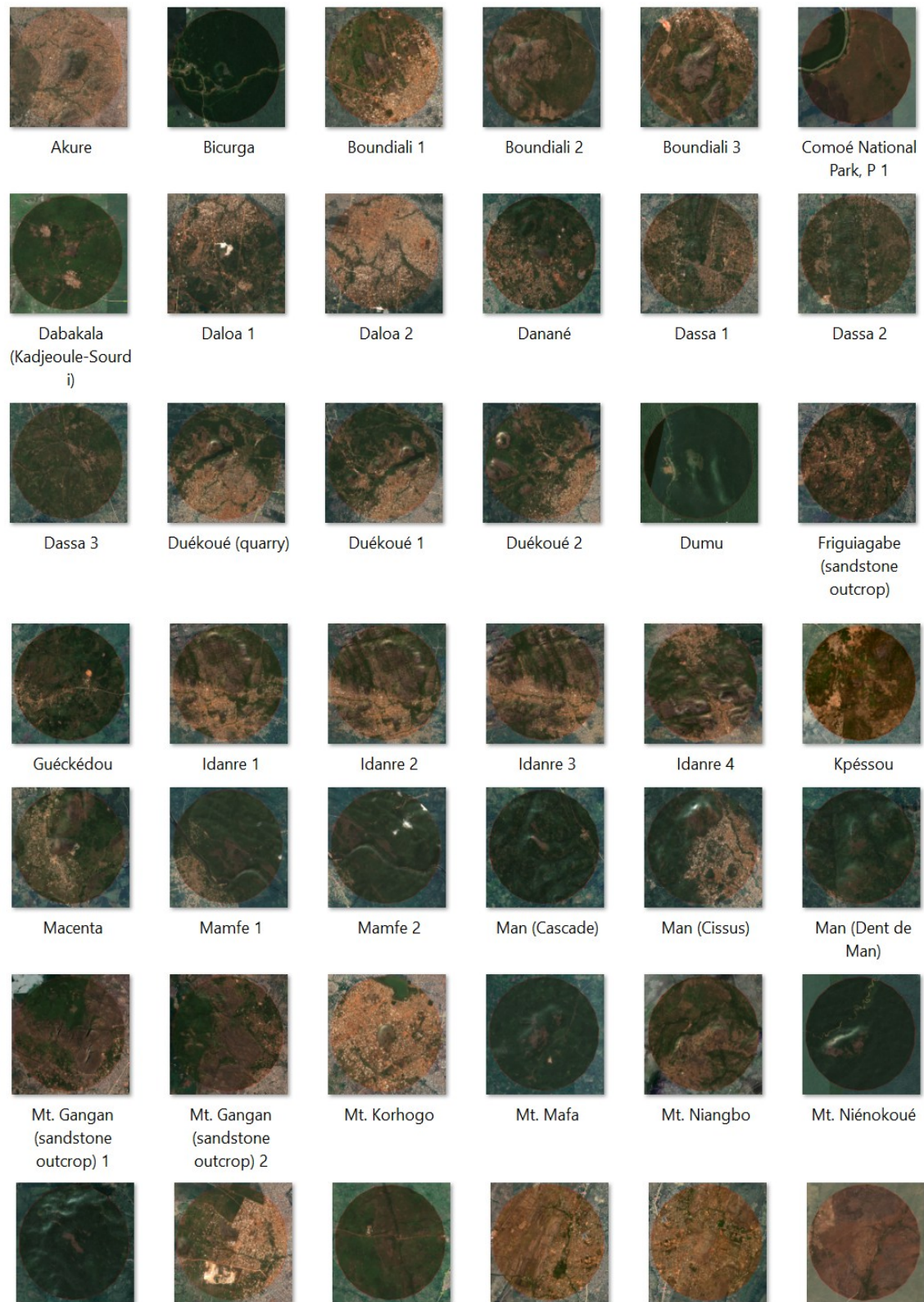
|                                      |           |          |   |   |   |   |   |   |   |   |   |   |
|--------------------------------------|-----------|----------|---|---|---|---|---|---|---|---|---|---|
| Duékoué (quarry)                     | -7.354167 | 6.754444 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| Sénéma (south of Séguéla)            | -6.58     | 7.7175   | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Mankono                         | -6.271667 | 8.098333 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Bouaké                          | -5.112778 | 7.762222 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| north of Boundiali                   | -6.466389 | 9.7275   | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| region of Abengourou (near Aniassué) | -3.717778 | 6.655    | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| region of Abengourou (near Atakro)   | -3.810556 | 6.667778 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| Mt. Mafa                             | -4.043611 | 5.8525   | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| near Foubolo                         | -4.670833 | 8.586111 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Mt. Tonkoui                          | -7.643889 | 7.4425   | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Comoé National Park, P 1             | -3.775    | 8.772222 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| P 13, south of Kakpin                | -3.777222 | 8.611389 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Lolobo                          | -5.306667 | 6.969444 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| west of Nassian                      | -3.4875   | 8.453611 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Brobo                           | -4.828611 | 7.662222 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Bouna (ferricrete)              | -3.038611 | 9.354167 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Odienné                         | -7.625556 | 9.679167 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Tiémé 1                         | -7.281667 | 9.554444 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Tiémé 2                         | -7.253889 | 9.559444 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Badandougou                     | -7.156944 | 9.570278 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Madinani 1                      | -7.013333 | 9.629167 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Madinani 2                      | -6.813333 | 9.594444 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Madinani 3                      | -6.737778 | 9.595556 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Gbando 1                        | -6.668333 | 9.556389 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Gbando 2                        | -6.659722 | 9.544167 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| near Touba (sandstone outcrop)       | -7.631111 | 8.228056 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |



|                                     |           |           |   |   |   |   |   |   |   |   |   |   |
|-------------------------------------|-----------|-----------|---|---|---|---|---|---|---|---|---|---|
| Daloa 1                             | -6.434722 | 6.829444  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Daloa 2                             | -6.434167 | 6.849722  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Sikensi 1                           | -4.561667 | 5.645     | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Sikensi 3                           | -4.5575   | 5.653611  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| near Tehini                         | -3.608056 | 9.595278  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Tehini (ferricrete)            | -3.58     | 9.607778  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Tondoura (BF)                  | -4.773611 | 10.173889 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Mangodara (BF)                 | -4.441667 | 9.857222  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Wayen (BF)                     | -0.983333 | 12.323611 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| near Zorgho (BF)                    | -0.632222 | 12.211111 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| near Léo (BF)                       | -2.193611 | 11.115833 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| Nazinga (BF)                        | -1.6075   | 11.178611 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| near Bobo-Dioulasso                 | -4.135278 | 11.303611 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| near Banfora (BF) sandstone         | -4.595833 | 10.848889 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Reserve de Bontioli (BF) ferricrete | -2.955556 | 10.944167 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| near Po 1                           | -1.123056 | 11.124722 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| near Po 2                           | -1.084167 | 11.073611 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| Soubakpérou (Benin)                 | 2.160278  | 9.144444  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Savé (Benin)                   | 2.163056  | 9.144444  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Kandi 1                        | 2.895556  | 11.130833 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| near Kandi 2                        | 2.900278  | 11.108333 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| near Goungoun (ferricrete) 1        | 3.154444  | 11.574167 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| near Goungoun (ferricrete) 2        | 3.150556  | 11.565    | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| near Goungoun (ferricrete) 3        | 3.160278  | 11.543333 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| Dassa 1                             | 2.190833  | 7.782222  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Dassa 2                             | 2.195278  | 7.753333  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Dassa 3                             | 2.202222  | 7.709722  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |

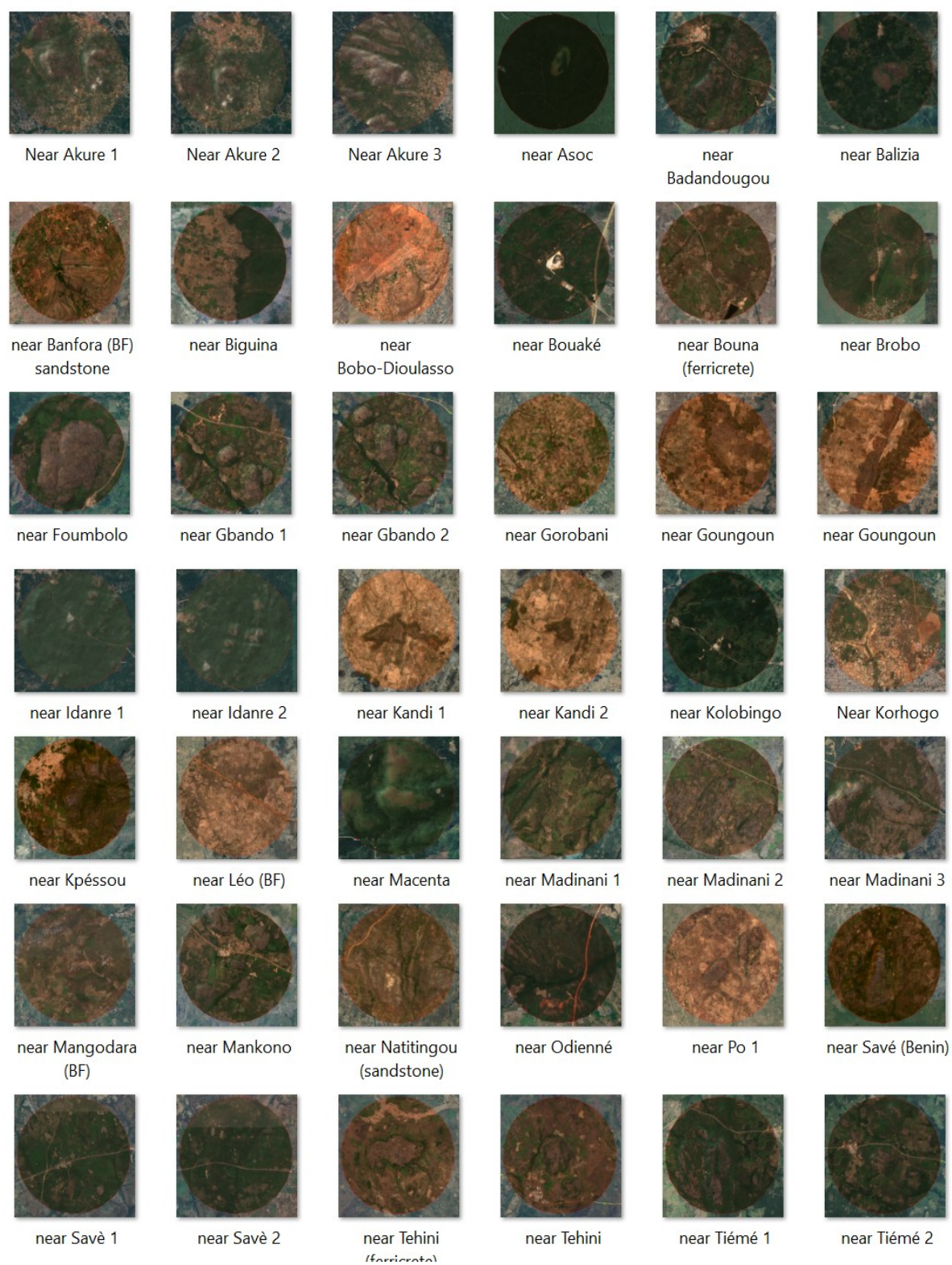
|                                  |            |           |   |   |   |   |   |   |   |   |   |   |
|----------------------------------|------------|-----------|---|---|---|---|---|---|---|---|---|---|
| Savalou                          | 1.978333   | 7.965833  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Natitingou (sandstone) 1         | 1.369167   | 10.306389 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Natitingou (sandstone) 2         | 1.395      | 10.301111 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Natitingou (sandstone)      | 1.444167   | 10.210833 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Biguina                     | 1.696667   | 8.764722  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Savè                             | 2.508056   | 8.036389  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Savè 1                      | 2.581944   | 8.04      | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Savè 2                      | 2.61       | 8.044722  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Gorobani:                   | 2.026389   | 9.4775    | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Yebessi                     | 2.105278   | 9.346667  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Yebessi                          | 2.133056   | 9.326111  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| near Kpéssou                     | 2.196111   | 9.296111  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Kpéssou                          | 2.188611   | 9.285556  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Yaounde 1                        | 11.393333  | 3.828056  | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| Yaounde 2                        | 11.425556  | 3.830278  | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| Yaounde 3                        | 11.434167  | 3.887778  | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| Yaounde 4                        | 11.443056  | 3.827222  | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| Yaounde 5                        | 11.466389  | 3.853056  | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| Mamfe 1                          | 9.322778   | 5.766111  | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| Mamfe 2                          | 9.336944   | 5.758333  | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| Takamanda 1                      | 9.513889   | 6.175833  | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| Takamanda 2                      | 9.525833   | 6.111944  | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| Friguiagabe (sandstone outcrop)  | -12.912778 | 9.976389  | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| Mt. Gangan (sandstone outcrop) 1 | -12.893056 | 10.055    | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| Mt. Gangan (sandstone outcrop) 2 | -12.878611 | 10.078056 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| Macenta                          | -9.460556  | 8.522222  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| near Macenta                     | -9.491667  | 8.599167  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |

|                |            |           |   |   |   |   |   |   |   |   |   |   |
|----------------|------------|-----------|---|---|---|---|---|---|---|---|---|---|
| near Balizia   | -9.605     | 8.601111  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Guéckédou      | -10.098611 | 8.557222  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| near Kolobingo | -10.017222 | 8.553611  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| near Técoulo   | -9.984444  | 8.534167  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Tongo Hills 1  | -0.812778  | 10.67     | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| Tongo Hills 2  | -0.803611  | 10.688889 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| Akure          | 5.181944   | 7.216389  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| Near Akure 1   | 5.161389   | 7.343333  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| Near Akure 2   | 5.171389   | 7.348611  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| Near Akure 3   | 5.226389   | 7.374167  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| Idanre 1       | 5.15       | 7.108889  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Idanre 2       | 5.144722   | 7.111389  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Idanre 3       | 5.133056   | 7.110833  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Idanre 4       | 5.105556   | 7.126667  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| near Idanre 1  | 5.034167   | 7.175278  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| near Idanre 2  | 5.0425     | 7.190278  | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| Bicurga        | 10.471111  | 1.583611  | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Piedras Nzas 1 | 11.031944  | 1.456389  | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Piedras Nzas 2 | 11.021667  | 1.463889  | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Dumu           | 11.323611  | 1.368056  | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| near Asoc      | 11.276944  | 1.451111  | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |

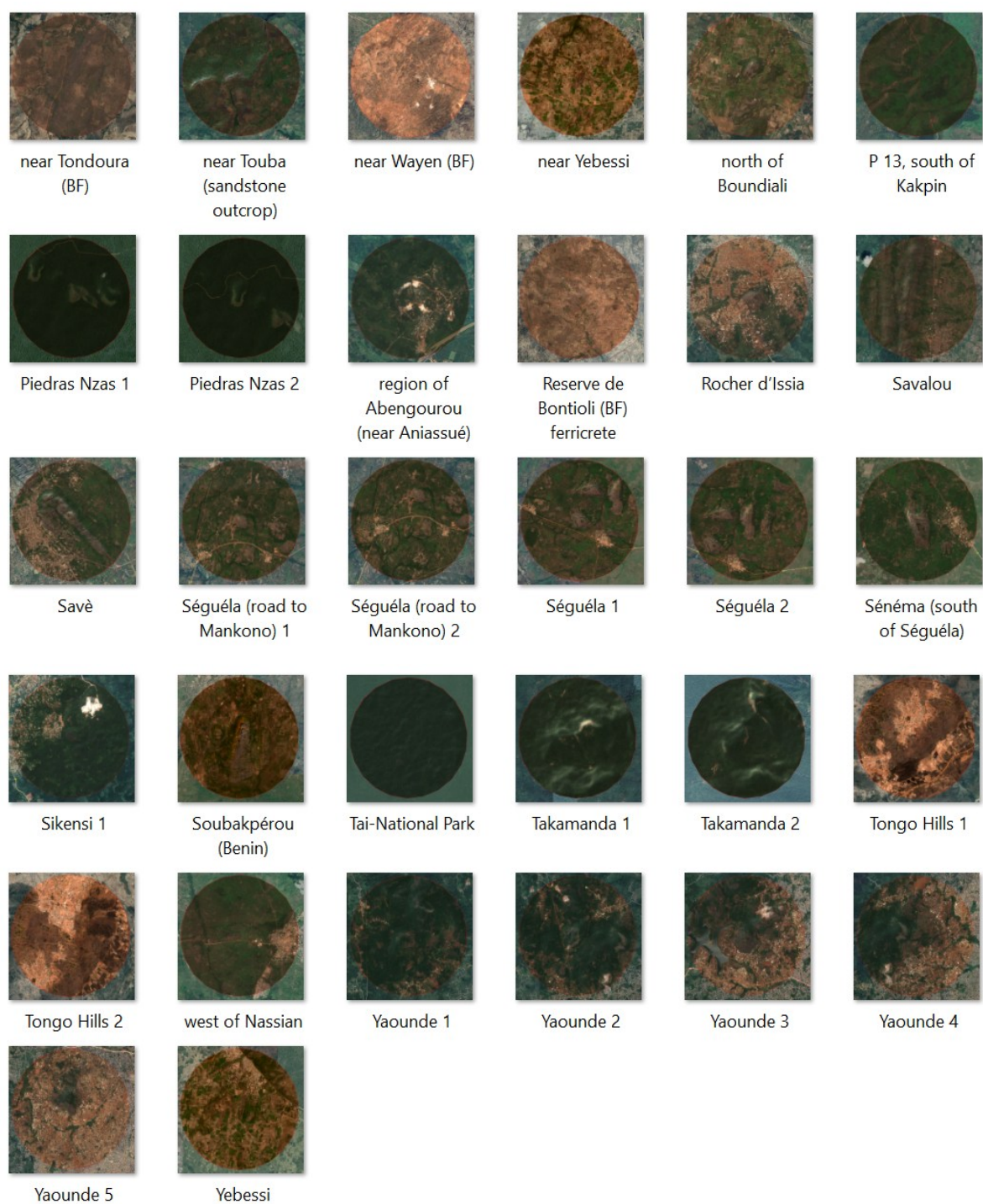


**Figure A 3.** Assessment of quarrying activities on inselbergs 1-42 across West Africa, distinguishing inselbergs with and without quarrying, using Google Earth Engine imagery.





**Figure A 4.** Assessment of quarrying activities on inselbergs 43-84 across West Africa, distinguishing inselbergs with and without quarrying, using Google Earth Engine imagery.



**Figure A 5.** Assessment of quarrying activities on inselbergs 84-123 across West Africa, distinguishing inselbergs with and without quarrying, using Google Earth Engine imagery.

**Table A6:** Species exposure to two anthropogenic drivers of biodiversity loss: quarrying and climate change. The evaluated species are *Asplenium stuhlmannii* (Aspleniaceae), *Phymathosorus scolopendria* (Polypodiaceae), *Pellaea doniana* (Pteridaceae), *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae), *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minima*, and *Sporobolus festivus* (Poaceae), and *Craterostigma yaundense* (Linderniaceae).

| Species                |                 | Exposure               |                 |  |
|------------------------|-----------------|------------------------|-----------------|--|
| Quarrying              |                 |                        |                 |  |
| <i>A. pilosa</i>       |                 | 10.75% (10 out of 93)  |                 |  |
| <i>A. stuhlmannii</i>  |                 | 10.75% (10 out of 93)  |                 |  |
| <i>C. yaundense</i>    |                 | 60% (3 out of 5)       |                 |  |
| <i>M. indica</i>       |                 | 8.89% (8 out of 90)    |                 |  |
| <i>M. squamosa</i>     |                 | 40% (4 out of 10)      |                 |  |
| <i>O. aristatum</i>    |                 | 13.33% (2 out of 15)   |                 |  |
| <i>P. doniana</i>      |                 | 13.64% (15 out of 110) |                 |  |
| <i>P. scolopendria</i> |                 | 14.63% (6 out of 41)   |                 |  |
| <i>S. festivus</i>     |                 | 8.26% (9 out of 109)   |                 |  |
| <i>T. minima</i>       |                 | 7.04% (5 out of 71)    |                 |  |
| Climate change         | 2011-2040       | 2041-2070              | 2071_2100       |  |
| SSP1                   |                 |                        |                 |  |
| <i>A. pilosa</i>       | 0.5 (0.4 - 0.6) | 1.4 (1.2 - 1.6)        | 1.4 (1.2 - 1.5) |  |
| <i>A. stuhlmannii</i>  | 0.6 (0.5 - 0.8) | 1.7 (1.6 - 2)          | 1.8 (1.6 - 2)   |  |
| <i>C. yaundense</i>    | 1.2 (1.2 - 1.2) | 3.5 (3.4 - 3.5)        | 3.8 (3.7 - 3.9) |  |
| <i>M. indica</i>       | 0.06 (0 - 0.1)  | 0.1 (0.1 - 0.1)        | 0.1 (0.1 - 0.2) |  |
| <i>M. squamosa</i>     | 0.9 (0.8 - 0.9) | 2.2 (2.1 - 2.3)        | 2.4 (2.2 - 2.5) |  |
| <i>O. aristatum</i>    | 0.5 (0.4 - 0.6) | 0.6 (0.6 - 0.8)        | 1.4 (1.3 - 1.6) |  |
| <i>P. doniana</i>      | 0.2 (0.1 - 0.3) | 0.2 (0.2 - 0.3)        | 0.5 (0.3 - 0.6) |  |
| <i>P. scolopendria</i> | 0.4 (0.3 - 0.5) | 1.1 (1 - 1.2)          | 1.2 (1 - 1.4)   |  |
| <i>S. festivus</i>     | 0.1 (0.1 - 0.2) | 0.4 (0.3 - 0.4)        | 0.4 (0.3 - 0.5) |  |
| <i>T. minima</i>       | 0.1 (0.1 - 0.2) | 0.4 (0.4 - 0.5)        | 0.4 (0.3 - 0.5) |  |
| SSP5                   |                 |                        |                 |  |
| <i>A. pilosa</i>       | 0.6 (0.5 - 0.7) | 3.9 (3.5 - 4.3)        | 13.2 (11 - 14)  |  |
| <i>A. stuhlmannii</i>  | 0.8 (0.6 - 0.9) | 5 (4.3 - 5.4)          | 16.6 (14 - 18)  |  |
| <i>C. yaundense</i>    | 1.4 (1.4 - 1.4) | 9.4 (9.3 - 9.4)        | 28.2 (28 - 28)  |  |
| <i>M. indica</i>       | 0.06 (0 - 0.1)  | 0.3 (0.3 - 0.4)        | 1.1 (0.9 - 1.2) |  |
| <i>M. squamosa</i>     | 1 (0.9 - 1.1)   | 6.5 (6.1 - 6.7)        | 21.4 (20 - 22)  |  |
| <i>O. aristatum</i>    | 0.7 (0.7 - 0.9) | 4.1 (3.9 - 4.8)        | 14.9 (14 - 17)  |  |
| <i>P. doniana</i>      | 0.2 (0.1 - 0.3) | 1.3 (0.9 - 1.5)        | 4.3 (3.7 - 4.8) |  |
| <i>P. scolopendria</i> | 0.5 (0.3 - 0.6) | 2.9 (2.5 - 3.2)        | 9.1 (7.9 - 9.7) |  |
| <i>S. festivus</i>     | 0.4 (0.3 - 0.5) | 1 (0.8 - 1.2)          | 3.4 (3 - 4)     |  |
| <i>T. minima</i>       | 0.2 (0.1 - 0.2) | 1.2 (0.9 - 1.3)        | 3.9 (3.4 - 4.6) |  |

**Table A7:** Species exposure to quarrying when comparing unprotected and protected inselbergs. The evaluated species are *Asplenium stuhlmannii* (Aspleniaceae), *Phymathosorus scolopendria* (Polypodiaceae), *Pellaea doniana* (Pteridaceae), *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae), *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minima*, and *Sporobolus festivus* (Poaceae), and *Craterostigma yaundense* (Linderniaceae).

| Species                | Number of unprotected inselbergs |                | Number of protected inselbergs |                |
|------------------------|----------------------------------|----------------|--------------------------------|----------------|
|                        | Without quarrying                | With quarrying | Without quarrying              | With quarrying |
| <i>A. pilosa</i>       | 69 (88%)                         | 9 (12%)        | 14 (93%)                       | 1 (7%)         |
| <i>A. stuhlmannii</i>  | 69 (88%)                         | 9 (12%)        | 14 (93%)                       | 1 (7%)         |
| <i>C. yaundense</i>    | 2 (40%)                          | 3 (60%)        | -                              | -              |
| <i>M. indica</i>       | 65 (90%)                         | 7 (10%)        | 17 (94%)                       | 1 (6%)         |
| <i>M. squamosa</i>     | 6 (60%)                          | 4 (40%)        | -                              | -              |
| <i>O. aristatum</i>    | 9 (82%)                          | 2 (18%)        | 4 (100%)                       | 0 (0%)         |
| <i>P. doniana</i>      | 78 (85%)                         | 14 (15%)       | 17 (94%)                       | 1 (6%)         |
| <i>P. scolopendria</i> | 30 (83%)                         | 6 (17%)        | 5 (100%)                       | 0 (0%)         |
| <i>S. festivus</i>     | 80 (91%)                         | 8 (9%)         | 20 (95%)                       | 1 (5%)         |
| <i>T. minima</i>       | 51 (93%)                         | 4 (7%)         | 15 (94%)                       | 1 (6%)         |



**Table A8:** Species exposure to climate change when comparing unprotected and protected inselbergs. The evaluated species are *Asplenium stuhlmannii* (Aspleniaceae), *Phymathosorus scolopendria* (Polypodiaceae), *Pellaea doniana* (Pteridaceae), *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae), *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minima*, and *Sporobolus festivus* (Poaceae), and *Craterostigma yaundense* (Linderniaceae).

| Species                | Unprotected inselbergs |                 |                 | Protected inselbergs |                 |                 |
|------------------------|------------------------|-----------------|-----------------|----------------------|-----------------|-----------------|
|                        | 2011-2040              | 2041-2070       | 2071_2100       | 2011-2041            | 2041-2071       | 2071_2101       |
| <b>SSP1</b>            |                        |                 |                 |                      |                 |                 |
| <i>A. pilosa</i>       | 0.5 (0.4 - 0.6)        | 1.4 (1.3 - 1.6) | 1.4 (1.2 - 1.5) | 0.5 (0.4 - 0.5)      | 1.3 (1.2 - 1.4) | 1.3 (1.2 - 1.4) |
| <i>A. stuhlmannii</i>  | 0.6 (0.5 - 0.8)        | 1.7 (1.6 - 2)   | 1.8 (1.6 - 2)   | 0.6 (0.5 - 0.7)      | 1.7 (1.6 - 1.8) | 1.7 (1.6 - 1.9) |
| <i>C. yaundense</i>    | 1.2 (1.2 - 1.2)        | 3.5 (3.4 - 3.5) | 3.9 (3.7 - 3.9) | -                    | -               | -               |
| <i>M. indica</i>       | 0.06 (< 0.1)           | 0.1 (0.1 - 0.1) | 0.1 (0.1 - 0.2) | 0.05 (< 0.1)         | 0.1 (0.1 - 0.1) | 0.1 (0.1 - 0.1) |
| <i>M. squamosa</i>     | 0.9 (0.8 - 0.9)        | 2.2 (2.1 - 2.3) | 2.4 (2.2 - 2.5) | -                    | -               | -               |
| <i>O. aristatum</i>    | 0.5 (0.4 - 0.6)        | 0.6 (0.6 - 0.8) | 1.4 (1.3 - 1.6) | 0.4 (0.4 - 0.4)      | 0.6 (0.6 - 0.6) | 1 (1 - 1.4)     |
| <i>P. doniana</i>      | 0.2 (0.1 - 0.3)        | 0.2 (0.2 - 0.3) | 0.5 (0.3 - 0.6) | 0.2 (0.1 - 0.2)      | 0.2 (0.2 - 0.2) | 0.5 (0.5 - 0.5) |
| <i>P. scolopendria</i> | 0.4 (0.3 - 0.5)        | 1.1 (1 - 1.2)   | 1.2 (1 - 1.4)   | 0.4 (0.4 - 0.4)      | 1.1 (1.1 - 1.1) | 1.2 (1 - 1.2)   |
| <i>S. festivus</i>     | 0.1 (0.1 - 0.2)        | 0.4 (0.3 - 0.4) | 0.4 (0.3 - 0.5) | 0.1 (0.1 - 0.1)      | 0.4 (0.3 - 0.4) | 0.4 (0.4 - 0.4) |
| <i>T. minima</i>       | 0.2 (0.1 - 0.2)        | 0.4 (0.4 - 0.5) | 0.4 (0.3 - 0.5) | 0.1 (0.1 - 0.2)      | 0.4 (0.4 - 0.4) | 0.4 (0.4 - 0.4) |
| <b>SSP5</b>            |                        |                 |                 |                      |                 |                 |
| <i>A. pilosa</i>       | 0.6 (0.5 - 0.7)        | 4 (3.5 - 4.3)   | 13.2 (11 - 14)  | 0.6 (0.5 - 0.7)      | 3.9 (3.6 - 4.1) | 13.2 (12 - 13)  |
| <i>A. stuhlmannii</i>  | 0.8 (0.6 - 0.9)        | 5 (4.3 - 5.4)   | 16.6 (14 - 18)  | 0.7 (0.6 - 0.8)      | 4.9 (4.5 - 5.1) | 16.7 (16 - 17)  |
| <i>C. yaundense</i>    | 1.4 (1.4 - 1.4)        | 9.4 (9.3 - 9.4) | 28.2 (28 - 28)  | -                    | -               | -               |
| <i>M. indica</i>       | 0.1 (0 - 0.1)          | 0.3 (0.3 - 0.4) | 1.1 (0.9 - 1.2) | 0.06 (0 - 0.1)       | 0.3 (0.3 - 0.4) | 1.1 (1 - 1.1)   |
| <i>M. squamosa</i>     | 1 (0.9 - 1.1)          | 6.5 (6.1 - 6.7) | 21.4 (20 - 22)  | -                    | -               | -               |
| <i>O. aristatum</i>    | 0.7 (0.7 - 0.9)        | 4.1 (3.9 - 4.8) | 15 (14 - 17)    | 0.7 (0.7 - 0.7)      | 4 (3.9 - 4)     | 14.5 (14 - 14)  |
| <i>P. doniana</i>      | 0.2 (0.1 - 0.3)        | 1.3 (0.9 - 1.5) | 4.3 (3.7 - 4.8) | 0.2 (0.2 - 0.2)      | 1.3 (1.2 - 1.3) | 4.3 (4.1 - 4.5) |
| <i>P. scolopendria</i> | 0.5 (0.3 - 0.6)        | 2.9 (2.5 - 3.2) | 9.1 (7.9 - 9.7) | 0.4 (0.4 - 0.5)      | 2.7 (2.5 - 2.9) | 8.7 (8.3 - 9.1) |
| <i>S. festivus</i>     | 0.4 (0.3 - 0.5)        | 1 (0.8 - 1.2)   | 3.5 (3 - 4)     | 0.4 (0.4 - 0.5)      | 1 (0.9 - 1.1)   | 3.4 (3.3 - 3.6) |
| <i>T. minima</i>       | 0.2 (0.1 - 0.2)        | 1.2 (0.9 - 1.3) | 4 (3.4 - 4.6)   | 0.2 (0.1 - 0.2)      | 1.1 (1 - 1.2)   | 3.9 (3.7 - 4)   |

## Appendix 3

**Table A10.** List of R packages used in this study

| R package         | Reference                                                                                                                                                                                                                                                                                                                                                                    |
|-------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| BAMMtools         | Rabosky, D. L., Grundler, M., Anderson, C., Title, P., Shi, J. J., Brown, J. W., ... & Larson, J. G. (2014). BAMM tools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. <i>Methods in Ecology and Evolution</i> , 5(7), 701–707. <a href="https://doi.org/10.1111/2041-210X.12199">https://doi.org/10.1111/2041-210X.12199</a>                |
| CoordinateCleaner | Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., ... & Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. <i>Methods in Ecology and Evolution</i> , 10(5), 744–751. <a href="https://doi.org/10.1111/2041-210X.13152">https://doi.org/10.1111/2041-210X.13152</a> |
| ggmap             | Kahle, D., & Wickham, H. (2013). ggmap: Spatial Visualization with ggplot2. R package.                                                                                                                                                                                                                                                                                       |
| ggplot2           | Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag. <a href="https://ggplot2.tidyverse.org">https://ggplot2.tidyverse.org</a>                                                                                                                                                                                                                  |
| humboldt          | Brown, J. L., & Carnaval, A. C. (2019). A tale of two niches: Methods, concepts, and evolution. <i>Frontiers of Biogeography</i> , 11(4). <a href="https://doi.org/10.21425/F5FBG44158">https://doi.org/10.21425/F5FBG44158</a>                                                                                                                                              |
| rnaturalearth     | South, A. (2017). rnaturalearth: World Map Data from Natural Earth. R package version 0.1.0. <a href="https://CRAN.R-project.org/package=rnaturalearth">https://CRAN.R-project.org/package=rnaturalearth</a>                                                                                                                                                                 |
| SDMtune           | Vignali, S., Barras, A. G., Arlettaz, R., & Braunisch, V. (2020). SDMtune: An R package to tune and evaluate species distribution models. <i>Ecology and Evolution</i> , 10(20), 11488–11506. <a href="https://doi.org/10.1002/ece3.6786">https://doi.org/10.1002/ece3.6786</a>                                                                                              |
| sf                | Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. <i>R Journal</i> , 10(1), 439–446. <a href="https://doi.org/10.32614/RJ-2018-009">https://doi.org/10.32614/RJ-2018-009</a>                                                                                                                                                          |
| terra             | Hijmans, R. (2023). terra: Spatial Data Analysis. R package version 1.7-65. <a href="https://CRAN.R-project.org/package=terra">https://CRAN.R-project.org/package=terra</a>                                                                                                                                                                                                  |
| usdm              | Naimi, B., Hamm, N. A., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? <i>Ecography</i> , 37, 191–203. <a href="https://doi.org/10.1111/j.1600-0587.2013.00205.x">https://doi.org/10.1111/j.1600-0587.2013.00205.x</a>                                                               |
| viridis           | Garnier, S. (2021). viridis: Default Color Maps from 'matplotlib'. R package version 0.6.4. <a href="https://CRAN.R-project.org/package=viridis">https://CRAN.R-project.org/package=viridis</a>                                                                                                                                                                              |

**Table A11.** Classes of diversity and endemism of desiccation-tolerant vascular plants. Jenks natural breaks was used for the classification.

|           | Diversity | Endemism            |
|-----------|-----------|---------------------|
| Very low  | 1-2       | 0.0000010-0.6931481 |
| Low       | 3-5       | 0.6931482-2.0794424 |
| Moderated | 6-11      | 2.0794425-3.4657368 |
| High      | 12-27     | 3.4657369-7.4217767 |
| Very high | 27-28     | 7.4217768-9.9111592 |

**Table A12.** The distribution area (in 10<sup>3</sup> km<sup>2</sup>) of desiccation-tolerant vascular plants in West Africa in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100). Positive values describe the contraction of areas of distribution, while negative values describe the contraction of areas of distribution.

| Species                  | Current | SSP1           |                |                | SSP5           |               |               |
|--------------------------|---------|----------------|----------------|----------------|----------------|---------------|---------------|
|                          |         | 2011 - 2040    | 2041 - 2070    | 2071 - 2100    | 2011 - 2040    | 2041 - 2070   | 2071 - 2100   |
| <i>A. aethiopicum</i>    | 70.1    | 38 (-46 %)     | 23.2 (-67 %)   | 20.4 (-71 %)   | 37.4 (-47 %)   | 11.8 (-83 %)  | 2.9 (-96 %)   |
| <i>A. friesiorum</i>     | 15.2    | 8.2 (-46 %)    | 4.9 (-68 %)    | 4.1 (-73 %)    | 9.2 (-40 %)    | 2.7 (-82 %)   | 0.9 (-94 %)   |
| <i>A. megalura</i>       | 220     | 115.8 (-47 %)  | 63.2 (-71 %)   | 59.6 (-73 %)   | 98.7 (-55 %)   | 27.6 (-87 %)  | 11.2 (-95 %)  |
| <i>A. monanthes</i>      | 1.4     | 1.1 (-28 %)    | 0.7 (-56 %)    | 0.5 (-67 %)    | 1.1 (-23 %)    | 0.4 (-72 %)   | 0.2 (-89 %)   |
| <i>A. sandersonii</i>    | 130.4   | 72.4 (-45 %)   | 52.7 (-60 %)   | 47.9 (-63 %)   | 70.8 (-46 %)   | 29.9 (-77 %)  | 10.4 (-92 %)  |
| <i>A. stuhlmannii</i>    | 1500.2  | 1300.9 (-13 %) | 1163.9 (-22 %) | 1116.4 (-26 %) | 1277.2 (-15 %) | 689.2 (-54 %) | 88.7 (-94 %)  |
| <i>A. pilosa</i>         | 1168.2  | 676.6 (-42 %)  | 399.7 (-66 %)  | 374.1 (-68 %)  | 628.8 (-46 %)  | 128.1 (-89 %) | 27.2 (-98 %)  |
| <i>C. abyssinica</i>     | 114.3   | 78.1 (-32 %)   | 67.1 (-41 %)   | 64.8 (-43 %)   | 74.5 (-35 %)   | 41.7 (-63 %)  | 21.1 (-82 %)  |
| <i>M. squamosa</i>       | 72.5    | 69.6 (-4 %)    | 74.9 (+3 %)    | 75.6 (+4 %)    | 60.9 (-16 %)   | 26.9 (-63 %)  | 12 (-83 %)    |
| <i>E. acrostichoides</i> | 3.4     | 3.1 (-11 %)    | 2.8 (-18 %)    | 2.6 (-26 %)    | 2.8 (-18 %)    | 2.2 (-37 %)   | 0.3 (-90 %)   |
| <i>H. capillare</i>      | 6.4     | 5.5 (-14 %)    | 5.3 (-18 %)    | 4.9 (-24 %)    | 5.5 (-15 %)    | 4.3 (-33 %)   | 2.8 (-56 %)   |
| <i>H. hirsutum</i>       | 214.9   | 117.1 (-45 %)  | 85.6 (-60 %)   | 76.4 (-64 %)   | 114.8 (-47 %)  | 50.3 (-77 %)  | 4.2 (-98 %)   |
| <i>H. kuhnii</i>         | 150.8   | 74.9 (-50 %)   | 40.5 (-73 %)   | 29.8 (-80 %)   | 70.8 (-53 %)   | 17.2 (-89 %)  | 5.7 (-96 %)   |
| <i>H. splendidum</i>     | 87.9    | 42.6 (-52 %)   | 28.2 (-68 %)   | 28.6 (-68 %)   | 43 (-51 %)     | 25.6 (-71 %)  | 12.1 (-86 %)  |
| <i>P. borbonicum</i>     | 178.9   | 122.7 (-31 %)  | 109.7 (-39 %)  | 106.7 (-40 %)  | 122.8 (-31 %)  | 78.3 (-56 %)  | 37 (-79 %)    |
| <i>C. chevalieri</i>     | 360.9   | 397.8 (+10 %)  | 386.1 (+7 %)   | 403.4 (+12 %)  | 353.3 (-2 %)   | 379.5 (+5 %)  | 397.9 (+10 %) |
| <i>D. erosum</i>         | 626.4   | 513.8 (-18 %)  | 474.7 (-24 %)  | 440.1 (-30 %)  | 524 (-16 %)    | 353.2 (-44 %) | 139.7 (-78 %) |
| <i>C. melanotrichum</i>  | 65.6    | 39.6 (-40 %)   | 28.5 (-57 %)   | 26.1 (-60 %)   | 39.5 (-40 %)   | 16.1 (-76 %)  | 5 (-92 %)     |
| <i>C. yaundense</i>      | 23.2    | 5 (-78 %)      | 0.2 (-99 %)    | 0.3 (-99 %)    | 1.2 (-95 %)    | 0 (-100 %)    | 0 (-100 %)    |
| <i>A. incisum</i>        | 36.6    | 18.4 (-50 %)   | 25 (-32 %)     | 19 (-48 %)     | 20.9 (-43 %)   | 18.3 (-50 %)  | 8.2 (-78 %)   |
| <i>A. radiata</i>        | 498     | 174.6 (-65 %)  | 75.8 (-85 %)   | 63.1 (-87 %)   | 135.5 (-73 %)  | 39.4 (-92 %)  | 9.5 (-98 %)   |

|                          |        |                |               |                |                |               |                |
|--------------------------|--------|----------------|---------------|----------------|----------------|---------------|----------------|
| <i>H. farinosa</i>       | 99.2   | 38.9 (-61 %)   | 25.2 (-75 %)  | 23.5 (-76 %)   | 35.1 (-65 %)   | 12.1 (-88 %)  | 3.9 (-96 %)    |
| <i>C. vellea</i>         | 6.3    | 6.4 (+1 %)     | 6.4 (+1 %)    | 6.4 (+1 %)     | 6.4 (+1 %)     | 6.4 (+1 %)    | 6.4 (+1 %)     |
| <i>M. flabelliformis</i> | 29.6   | 16.6 (-44 %)   | 11.5 (-61 %)  | 11 (-63 %)     | 14.8 (-50 %)   | 7.6 (-74 %)   | 2.4 (-92 %)    |
| <i>C. inaequalis</i>     | 4615   | 1.2 (-73 %)    | 0 (-100 %)    | 0 (-100 %)     | 0.6 (-86 %)    | 0 (-100 %)    | 0 (-100 %)     |
| <i>L. abyssinica</i>     | 558.3  | 244.1 (-56 %)  | 138.5 (-75 %) | 116.6 (-79 %)  | 240.3 (-57 %)  | 57.3 (-90 %)  | 19.2 (-97 %)   |
| <i>M. indica</i>         | 3013   | 3194.9 (+6 %)  | 3188 (+6 %)   | 3186.1 (+6 %)  | 3157.7 (+5 %)  | 3094.6 (+3 %) | 2710 (-10 %)   |
| <i>M. kunthii</i>        | 231.2  | 42.4 (-82 %)   | 10.5 (-95 %)  | 9 (-96 %)      | 23.6 (-90 %)   | 2.1 (-99 %)   | 0.1 (-100 %)   |
| <i>O. aristatum</i>      | 561.4  | 468.4 (-17 %)  | 518.7 (-8 %)  | 443.7 (-21 %)  | 536.5 (-4 %)   | 406.4 (-28 %) | 78.2 (-86 %)   |
| <i>P. dura</i>           | 21.8   | 20.4 (-7 %)    | 18.4 (-16 %)  | 17.4 (-20 %)   | 20.1 (-8 %)    | 11.3 (-48 %)  | 0 (-100 %)     |
| <i>P. macrocarpa</i>     | 49.2   | 30.9 (-37 %)   | 20.6 (-58 %)  | 19 (-61 %)     | 31.6 (-36 %)   | 12.7 (-74 %)  | 3.5 (-93 %)    |
| <i>P. scolopendria</i>   | 1618.9 | 1560.4 (-4 %)  | 1628.1 (+1 %) | 1584.1 (-2 %)  | 1456.2 (-10 %) | 1291 (-20 %)  | 1352.1 (-16 %) |
| <i>S. festivus</i>       | 1941.1 | 1650.4 (-15 %) | 1801.6 (-7 %) | 1720.4 (-11 %) | 1750.6 (-10 %) | 924.7 (-52 %) | 221.9 (-89 %)  |
| <i>S. pellucidus</i>     | 218.2  | 194.5 (-11 %)  | 228.9 (+5 %)  | 201.9 (-7 %)   | 186.4 (-15 %)  | 194.9 (-11 %) | 200.4 (-8 %)   |
| <i>P. stemaria</i>       | 1265.7 | 1222 (-3 %)    | 1163.9 (-8 %) | 1184 (-6 %)    | 1239.2 (-2 %)  | 1256.2 (-1 %) | 1067 (-16 %)   |
| <i>T. major</i>          | 66.4   | 57 (-14 %)     | 58.2 (-12 %)  | 59.5 (-10 %)   | 53.8 (-19 %)   | 49.4 (-26 %)  | 35.5 (-47 %)   |
| <i>T. minima</i>         | 1773.9 | 1722.7 (-3 %)  | 1782.8 (+1 %) | 1628.3 (-8 %)  | 1680.9 (-5 %)  | 574.7 (-68 %) | 38.2 (-98 %)   |
| <i>T. multiflorus</i>    | 32.7   | 21.1 (-36 %)   | 7.5 (-77 %)   | 7.4 (-77 %)    | 18.5 (-43 %)   | 2.4 (-93 %)   | 0 (-100 %)     |
| <i>V. guineensis</i>     | 780.8  | 533.6 (-32 %)  | 331.2 (-58 %) | 282.1 (-64 %)  | 539 (-31 %)    | 145.4 (-81 %) | 20.9 (-97 %)   |
| <i>S. njamnjamensis</i>  | 76.7   | 90 (+17 %)     | 102.8 (+34 %) | 98.4 (+28 %)   | 88.5 (+15 %)   | 89.9 (+17 %)  | 106.7 (+39 %)  |
| <i>A. orientalis</i>     | 509.3  | 172 (-66 %)    | 103.3 (-80 %) | 88.8 (-83 %)   | 168 (-67 %)    | 46.4 (-91 %)  | 13.1 (-97 %)   |
| <i>X. schnizleinia</i>   | 30.1   | 14.3 (-53 %)   | 5.9 (-80 %)   | 3 (-90 %)      | 12.2 (-60 %)   | 0.8 (-97 %)   | 0 (-100 %)     |

**Table 13.** The area (in 10<sup>3</sup> km<sup>2</sup>) of current diversity patterns and area shifts (in percentage) under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100). Positive values describe the contraction of areas of a given class of diversity and endemism, while negative values describe the contraction of areas of a given class of diversity and endemism.

|                   |         | SSP1           |                |                | SSP5           |                |                 |
|-------------------|---------|----------------|----------------|----------------|----------------|----------------|-----------------|
|                   | Current | 2011 - 2040    | 2041 - 2070    | 2071 - 2100    | 2011 - 2040    | 2041 - 2070    | 2071 - 2100     |
| Species richness  |         |                |                |                |                |                |                 |
| Very low          | 2493.6  | 3004 (+20 %)   | 3076.1 (+23 %) | 3175.8 (+27 %) | 3016.1 (+21 %) | 4100 (+64 %)   | 4060.8 (+63 %)  |
| Low               | 1574.6  | 1422.9 (-10 %) | 1423.6 (-10 %) | 1302.6 (-17 %) | 1402.9 (-11 %) | 578.9 (-63 %)  | 218.9 (-86 %)   |
| Moderate          | 568.7   | 323.0 (-43 %)  | 252.4 (-56 %)  | 234.4 (-59 %)  | 292.1 (-49 %)  | 95.8 (-83 %)   | 29.6 (-95 %)    |
| High              | 103.4   | 73.2 (-29 %)   | 51.5 (-50 %)   | 46.9 (-55 %)   | 66.1 (-36 %)   | 26.7 (-74 %)   | 10.6 (-90 %)    |
| Very High         | 0.02    | 0.02 (+25 %)   | 0 (-100 %)     | 0 (-100 %)     | 0 (-100 %)     | 0 (-100 %)     | 0 (-100 %)      |
| Endemism richness |         |                |                |                |                |                |                 |
| Very low          | 1407.7  | 1960.2 (+39 %) | 1961.9 (+39 %) | 2026.1 (+44 %) | 1798.2 (+28 %) | 2159.6 (+53 %) | 3082.1 (+119 %) |
| Low               | 2336.9  | 2146.9 (-8 %)  | 2250.5 (-4 %)  | 2198.6 (-6 %)  | 2287.2 (-2 %)  | 2214.1 (-5 %)  | 1204.6 (-48 %)  |
| Moderate          | 663.9   | 538.6 (-19 %)  | 524.9 (-21 %)  | 489.7 (-26 %)  | 517.8 (-22 %)  | 341.9 (-48 %)  | 387.4 (-42 %)   |
| High              | 331.7   | 265.3 (-20 %)  | 214.6 (-35 %)  | 198 (-40 %)    | 245.2 (-26 %)  | 172.6 (-48 %)  | 128.4 (-61 %)   |
| Very High         | 0.1     | 0.8 (+628 %)   | 0.9 (+694 %)   | 0.9 (+710 %)   | 1.6 (+1313 %)  | 1.5 (+1251 %)  | 4.3 (+3765 %)   |

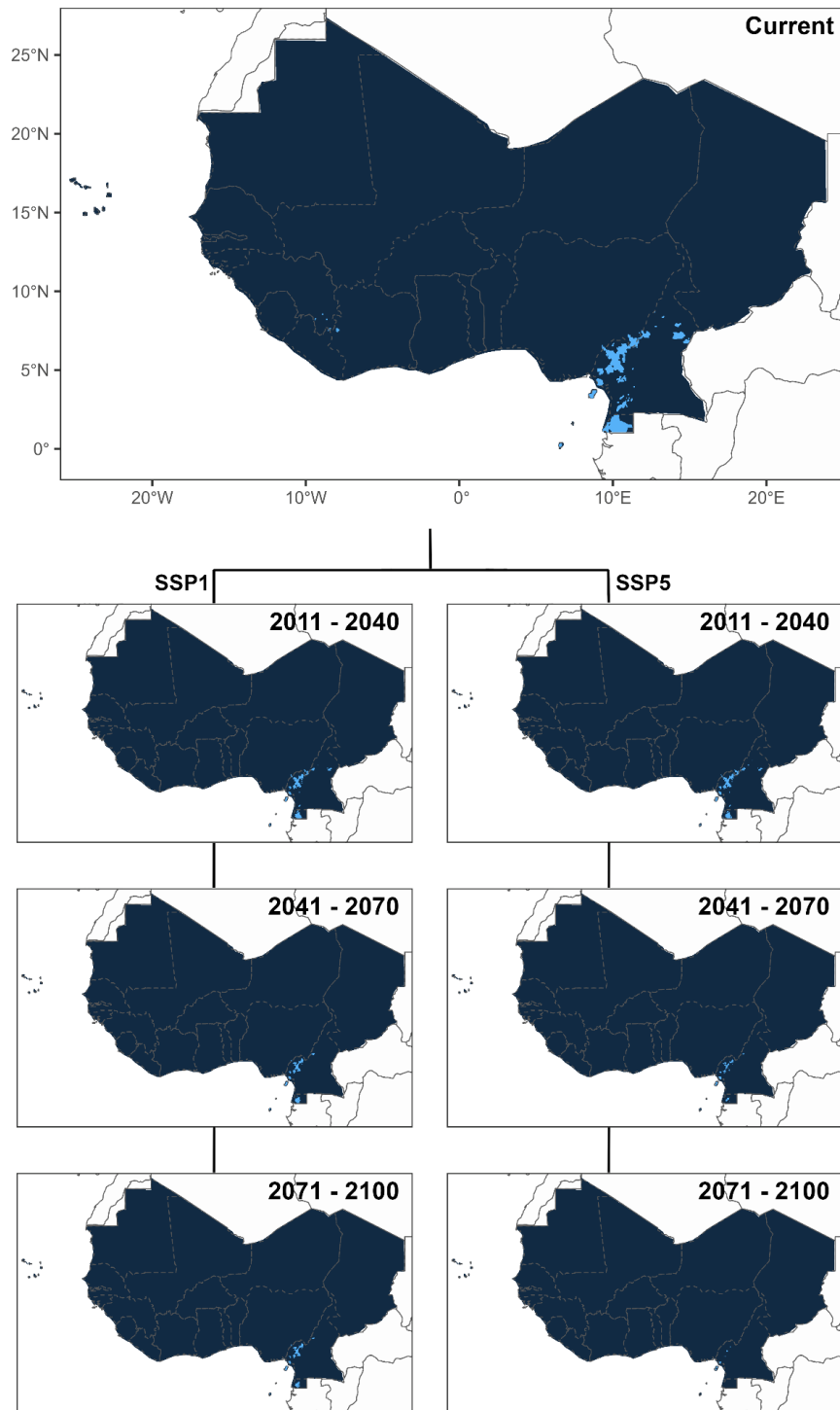


Figure A 6: The distribution hypotheses of *Asplenium aethiopicum* (Aspleniaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

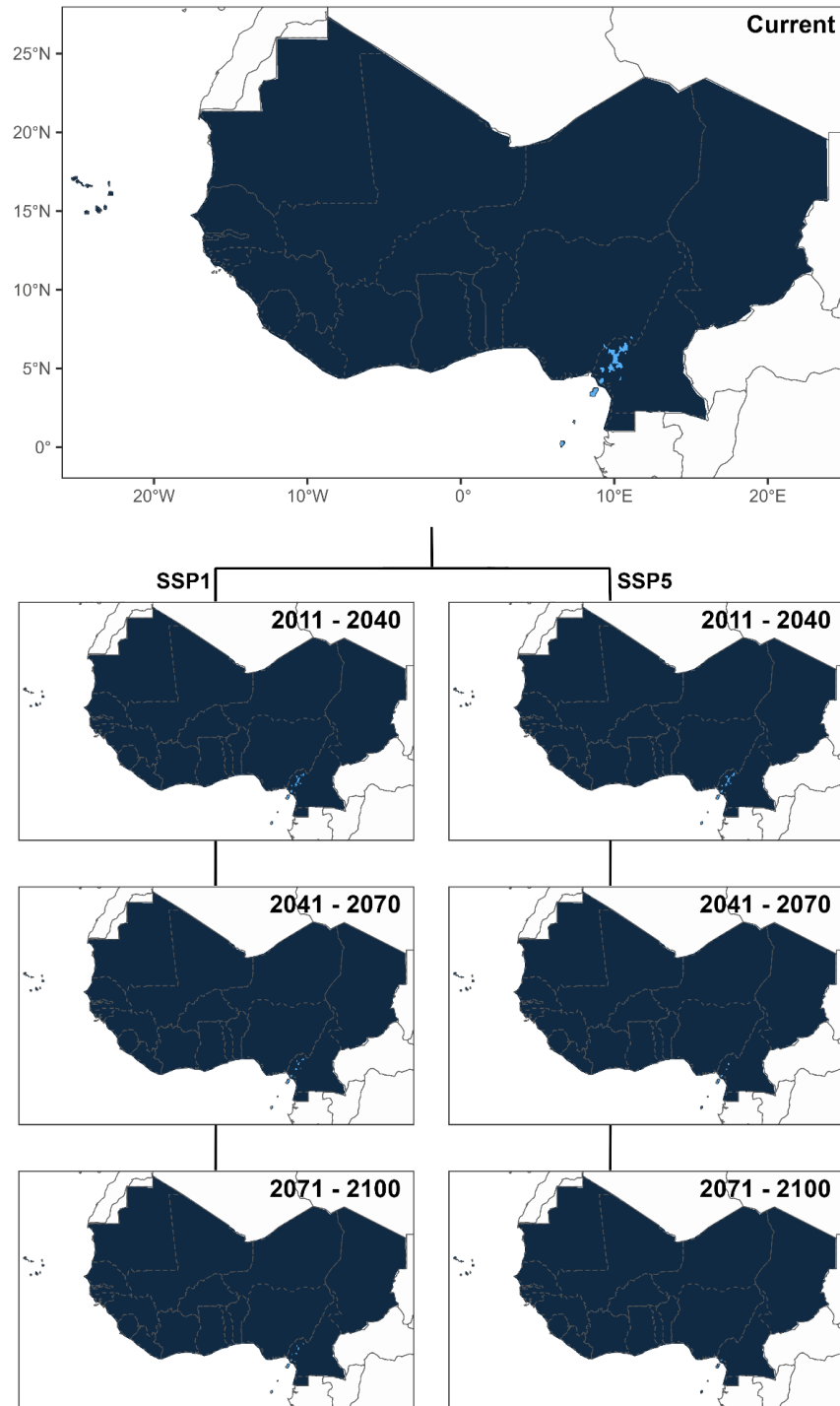


Figure A 7: The distribution hypotheses of *Asplenium friesiorum* (Aspleniaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

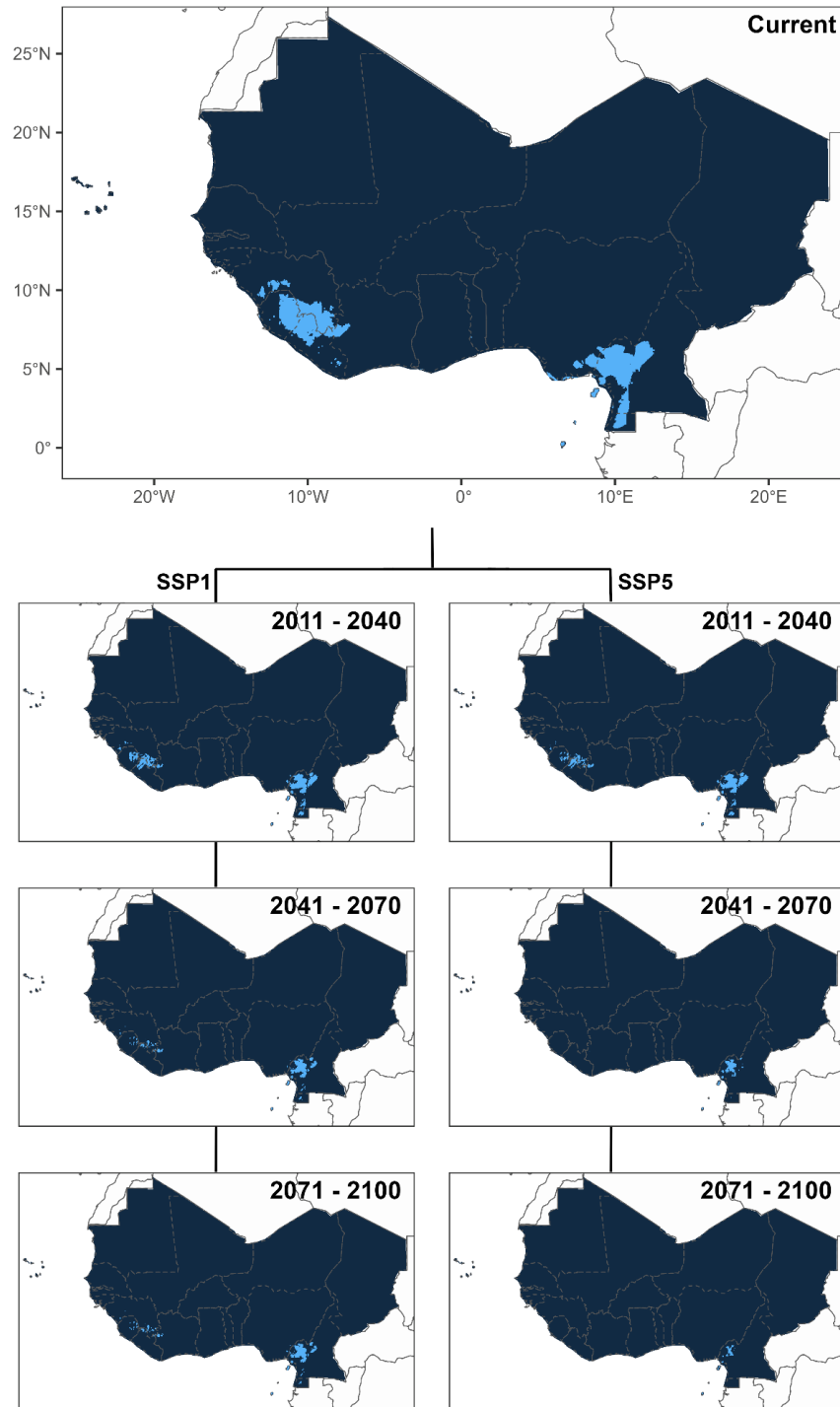


Figure A 8: The distribution hypotheses of *Asplenium megalura* (Aspleniaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).



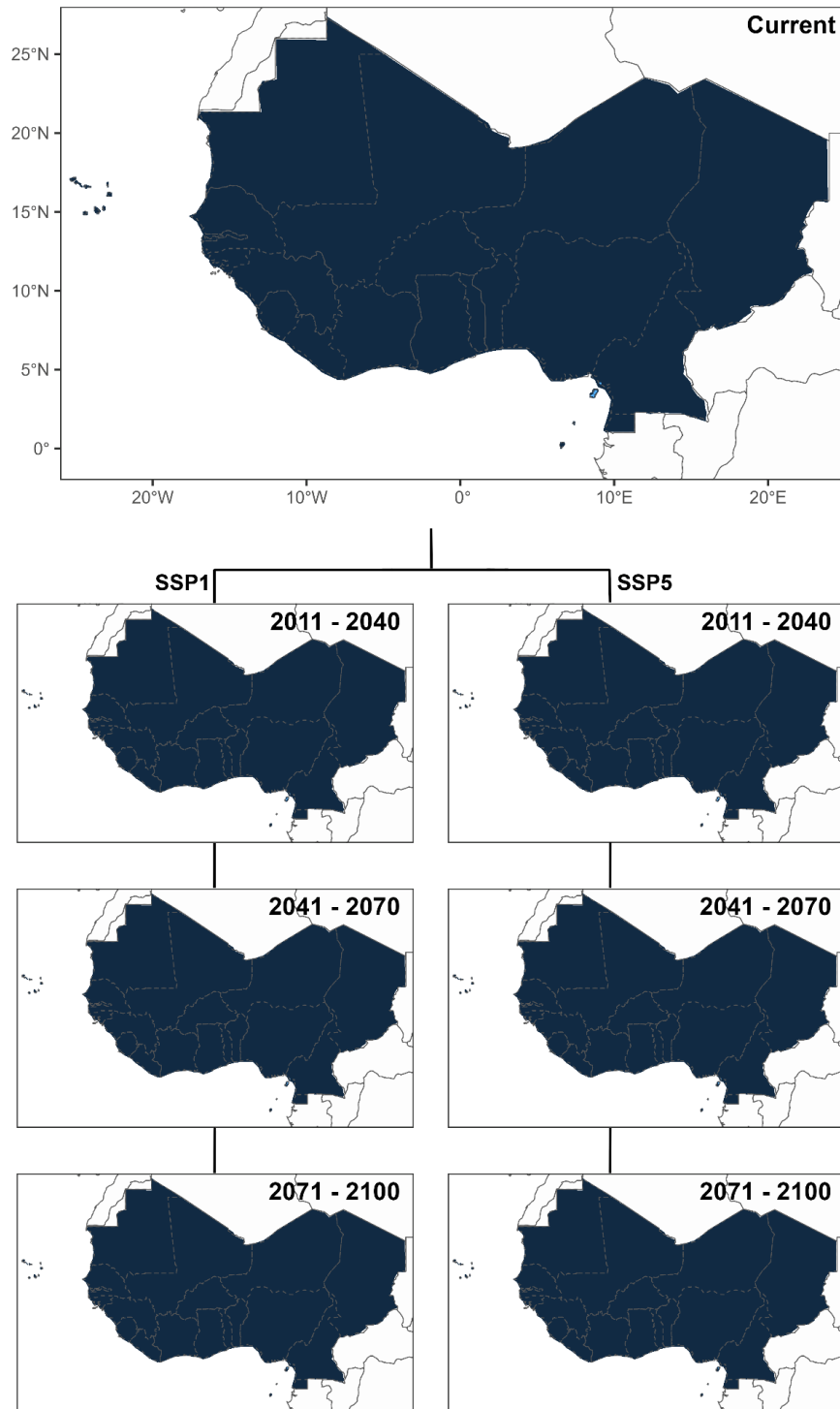


Figure A 9: The distribution hypotheses of *Asplenium monanthes* (Aspleniaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

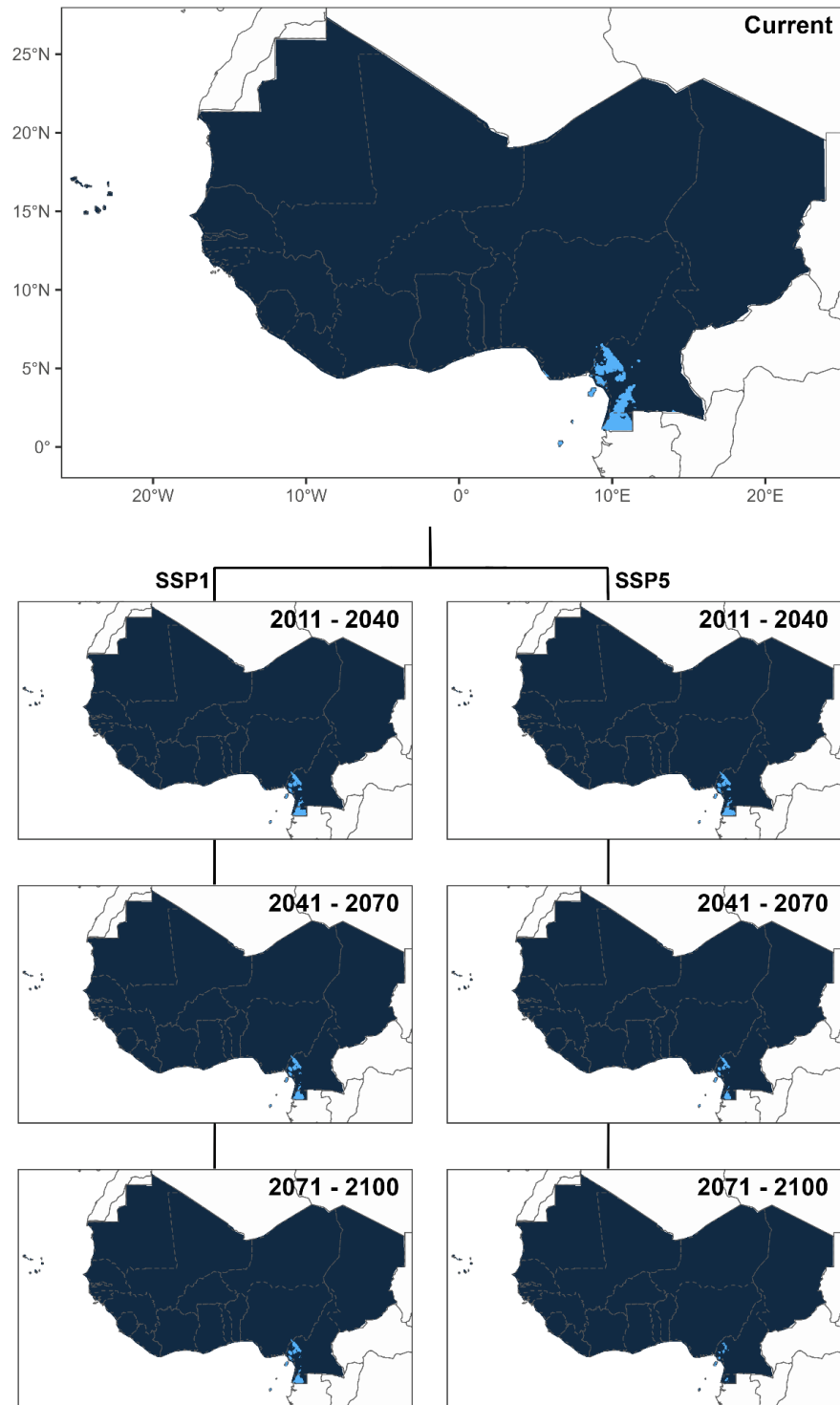


Figure A 10: The distribution hypotheses of *Asplenium sandersonii* (Aspleniaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

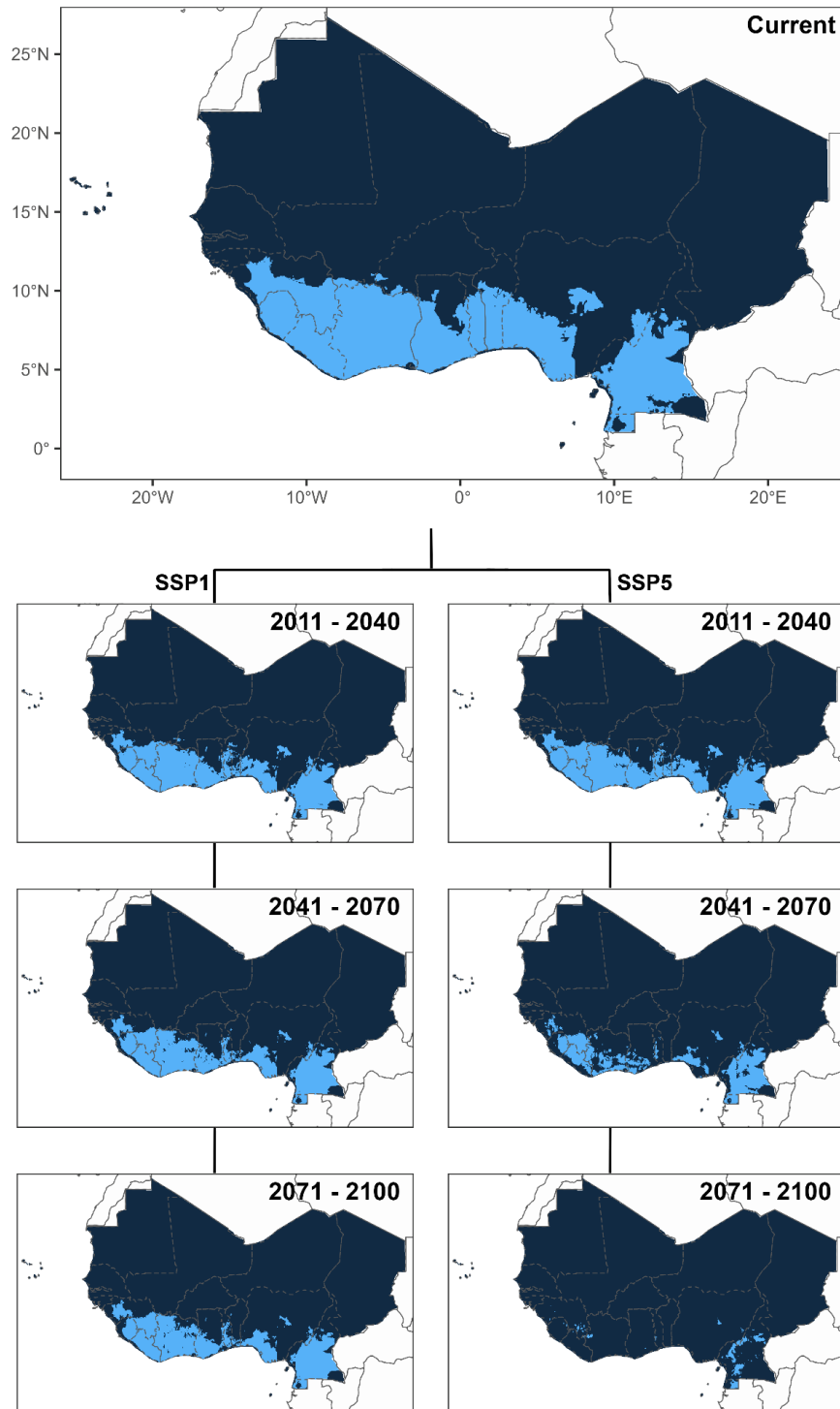


Figure A 11: The distribution hypotheses of *Asplenium stuhlmannii* (Aspleniaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

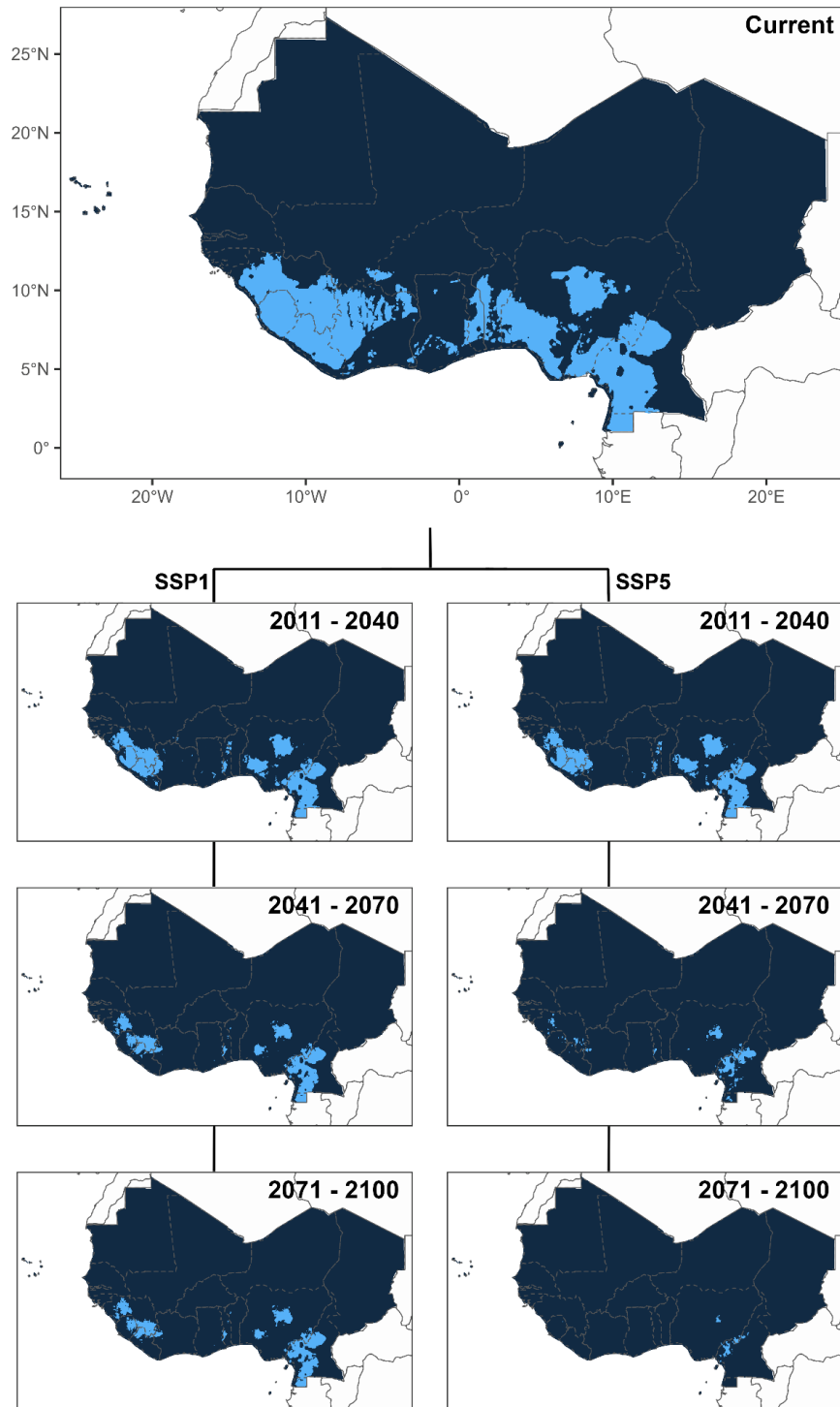


Figure A 12: The distribution hypotheses of *Afrotrilepis pilosa* (Cyperaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

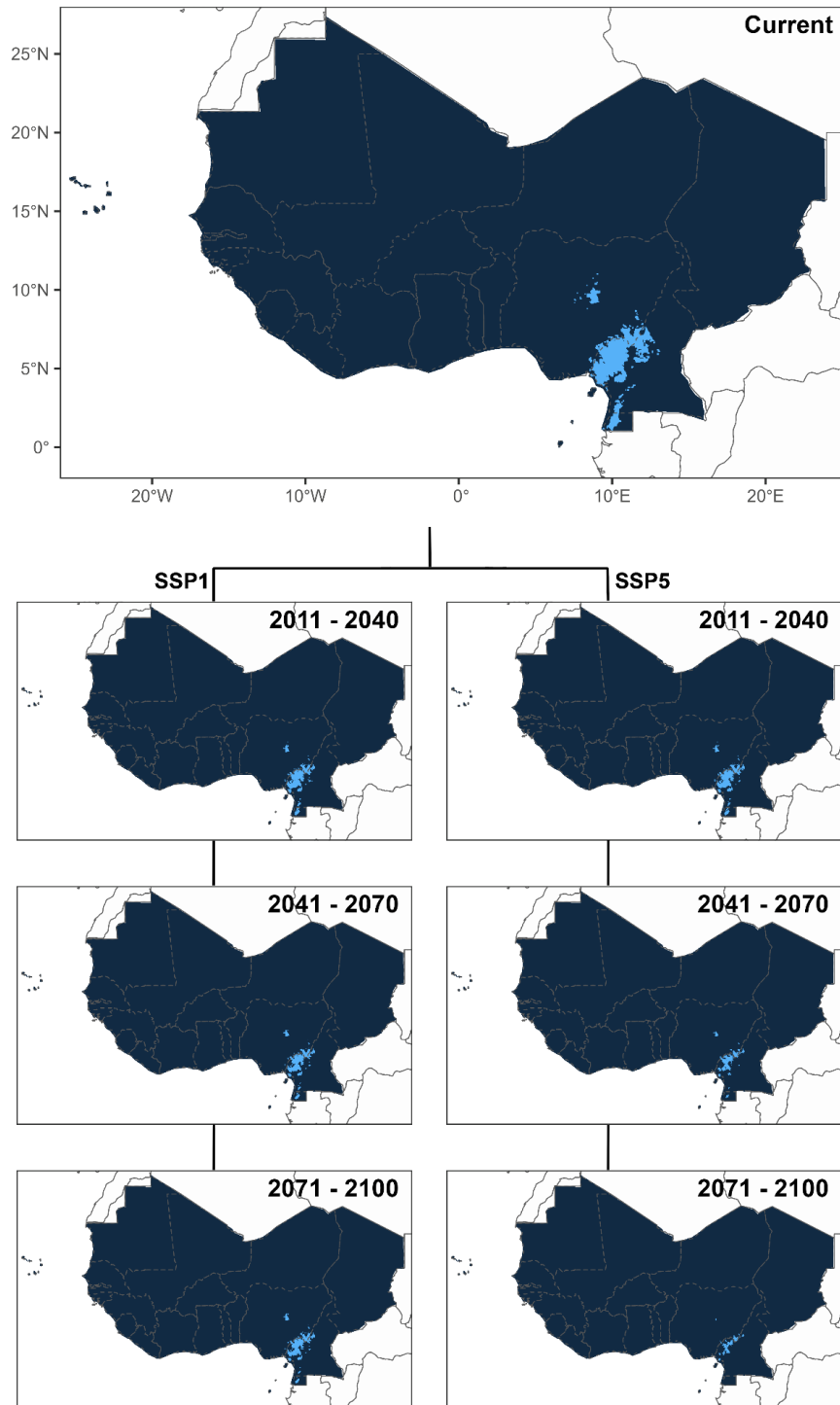


Figure A 13: The distribution hypotheses of *Coleochloa abyssinica* (Cyperaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

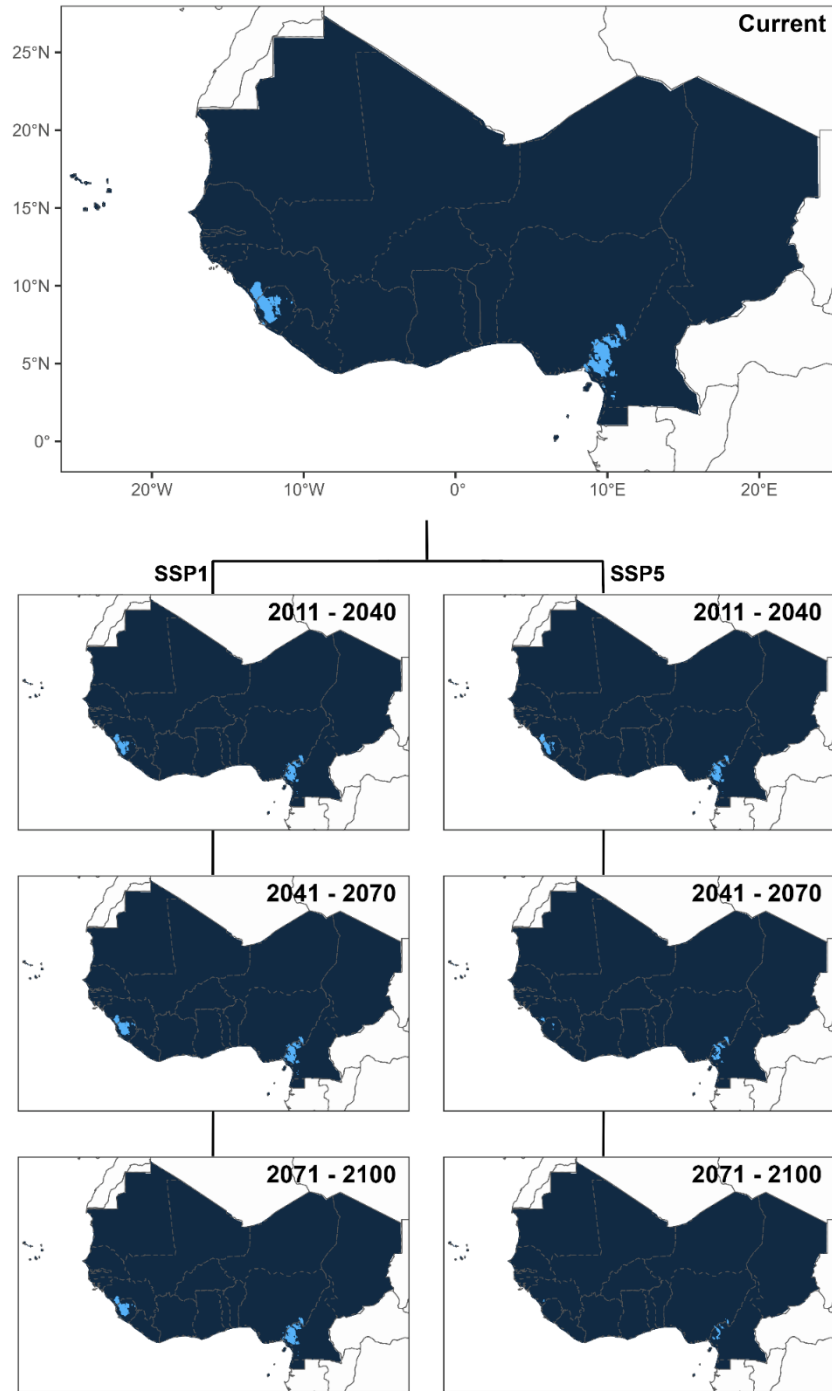


Figure A 14: The distribution hypotheses of *Microdracoides squamosa* (Cyperaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

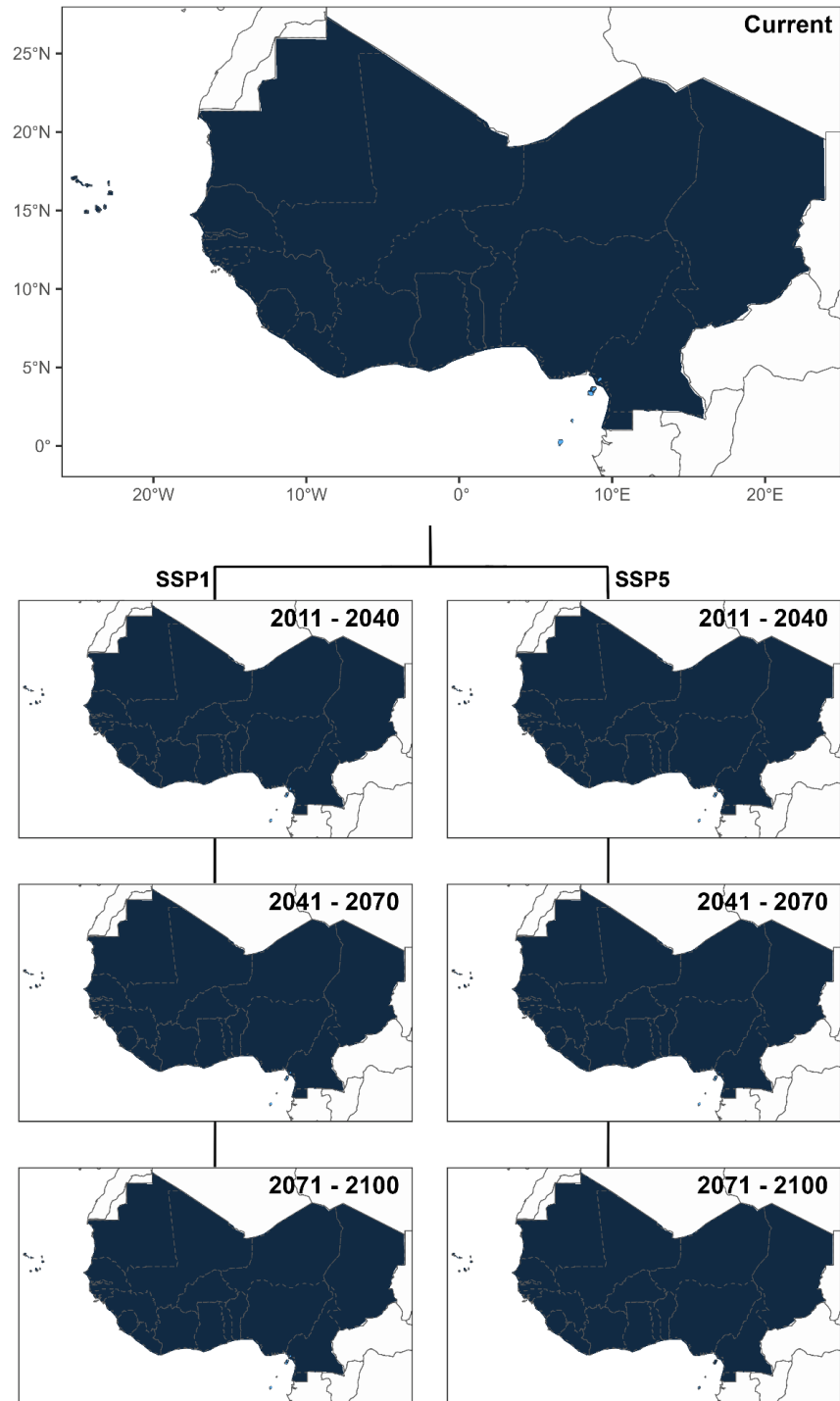


Figure A 15: The distribution hypotheses of *Elaphoglossum acrostichoides* (Dryopteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

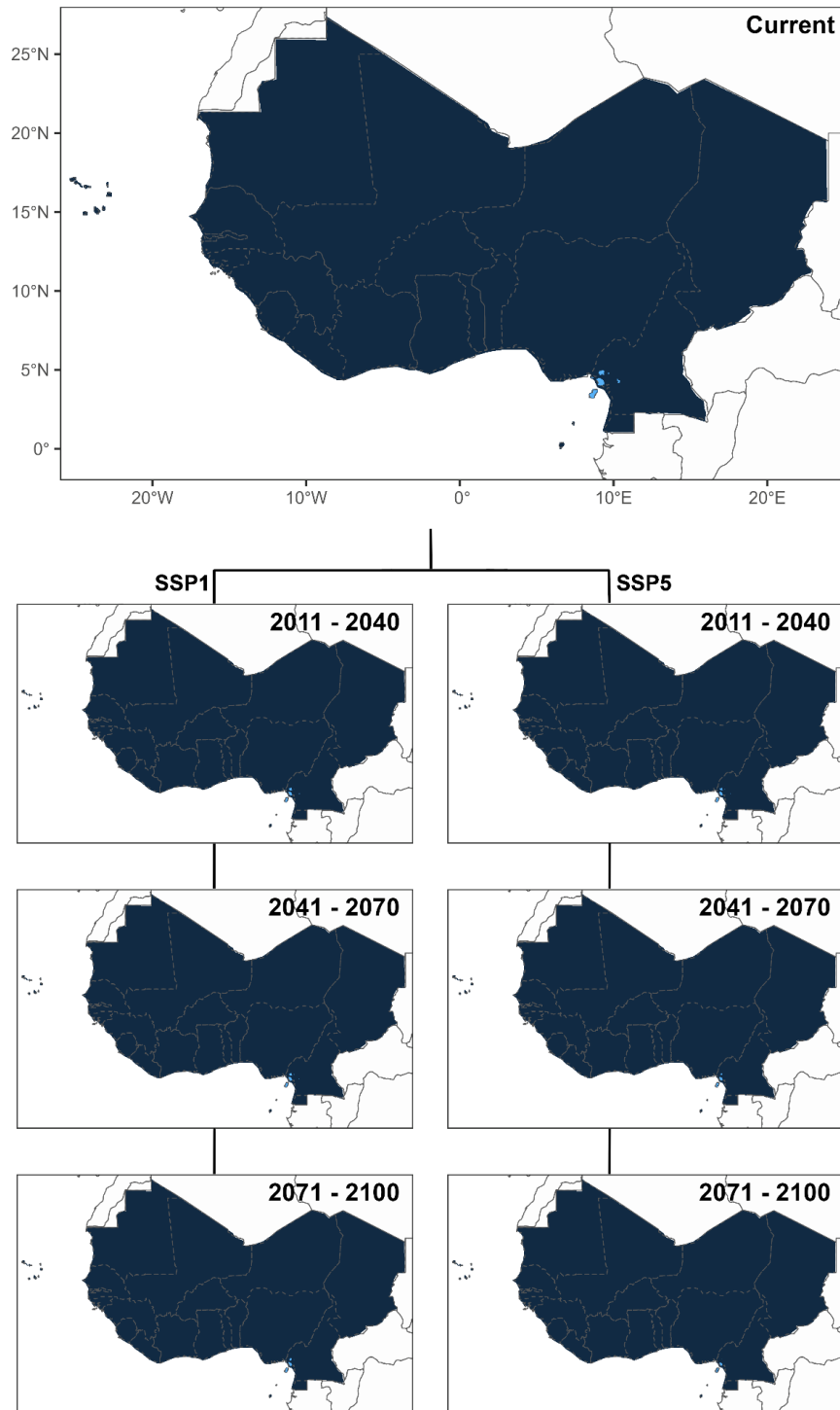


Figure A 16: The distribution hypotheses of *Hymenophyllum capillare* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).



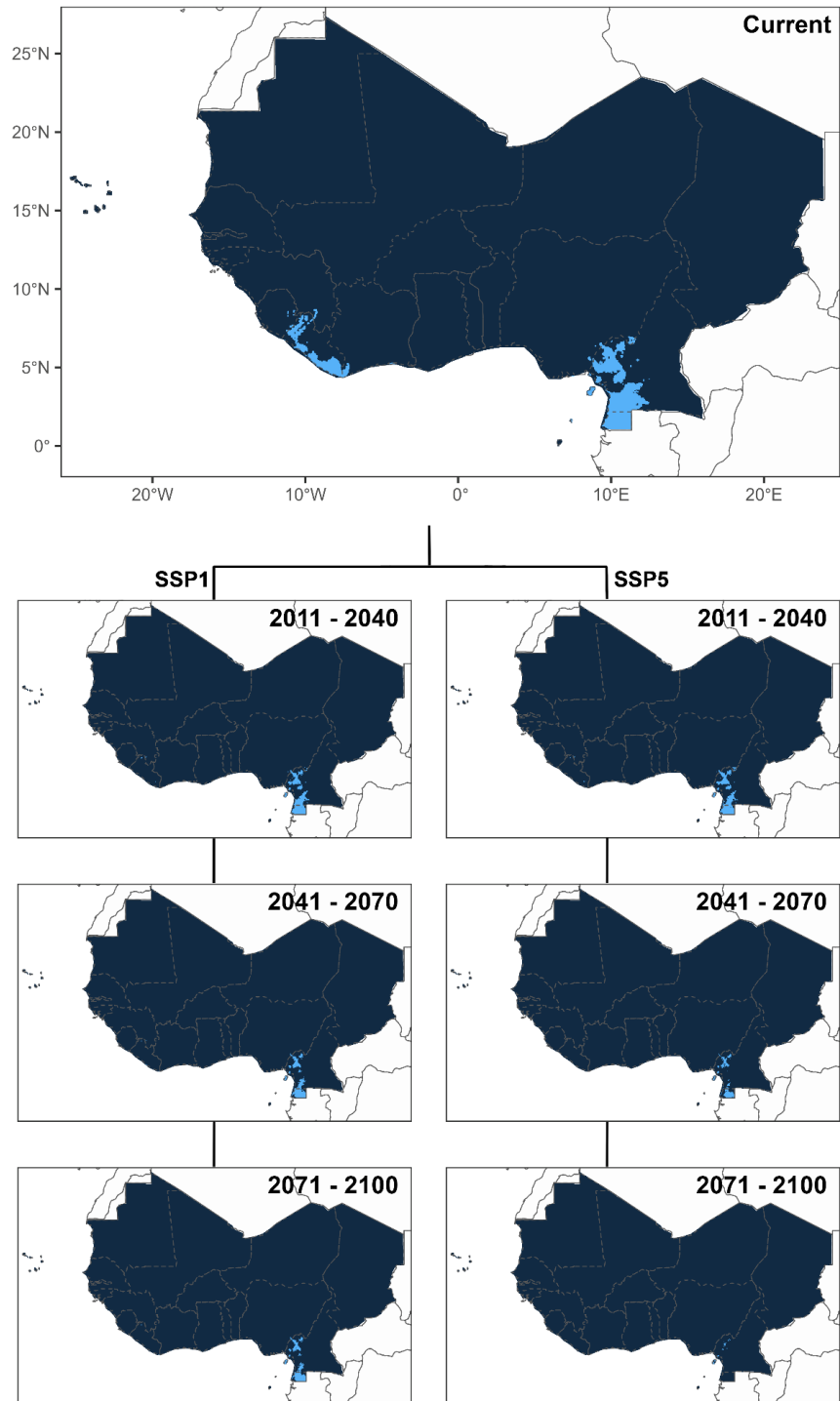


Figure A 17: The distribution hypotheses of *Hymenophyllum hirsutum* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

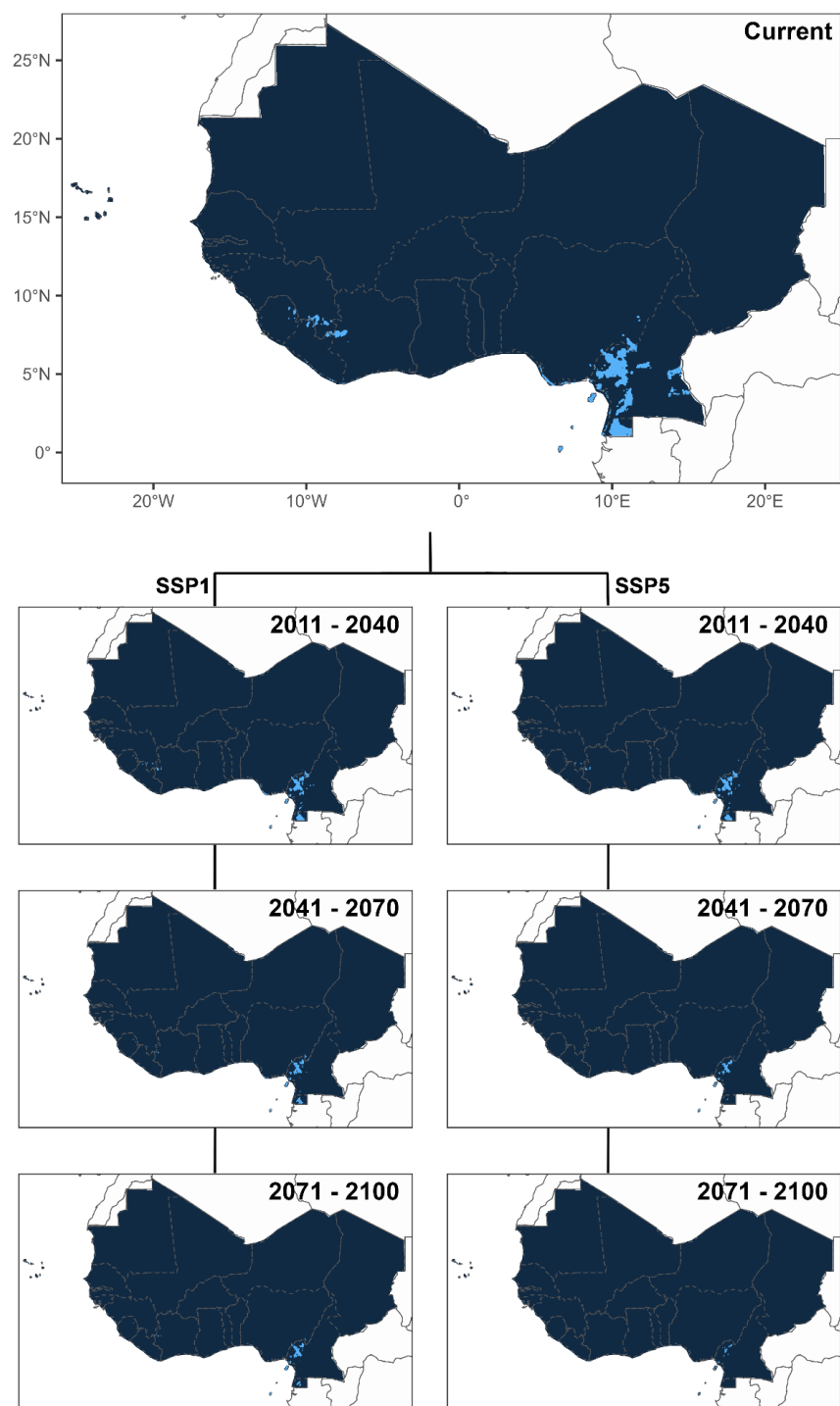


Figure A 18: The distribution hypotheses of *Hymenophyllum kuhnii* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

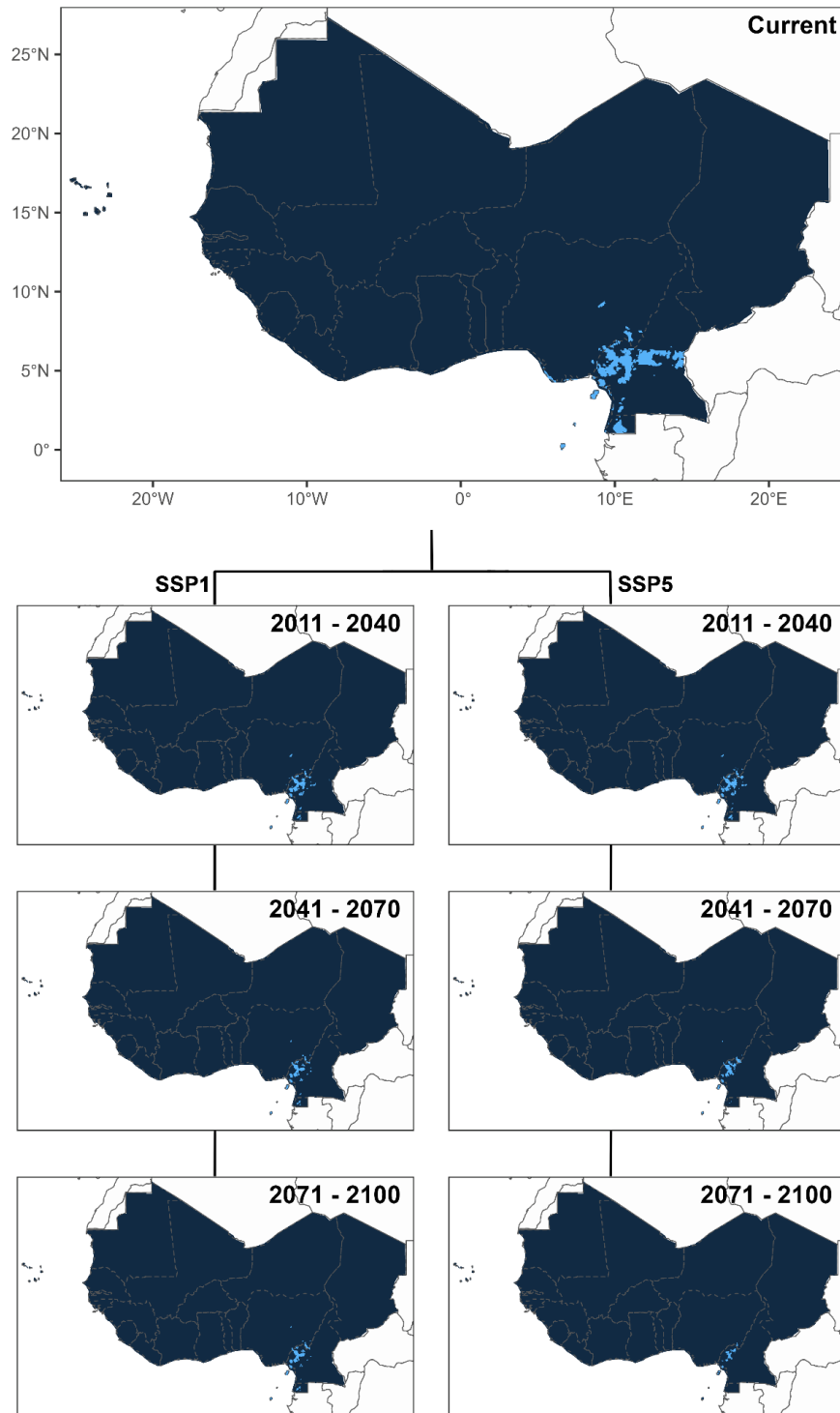


Figure A 19: The distribution hypotheses of *Hymenophyllum splendidum* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

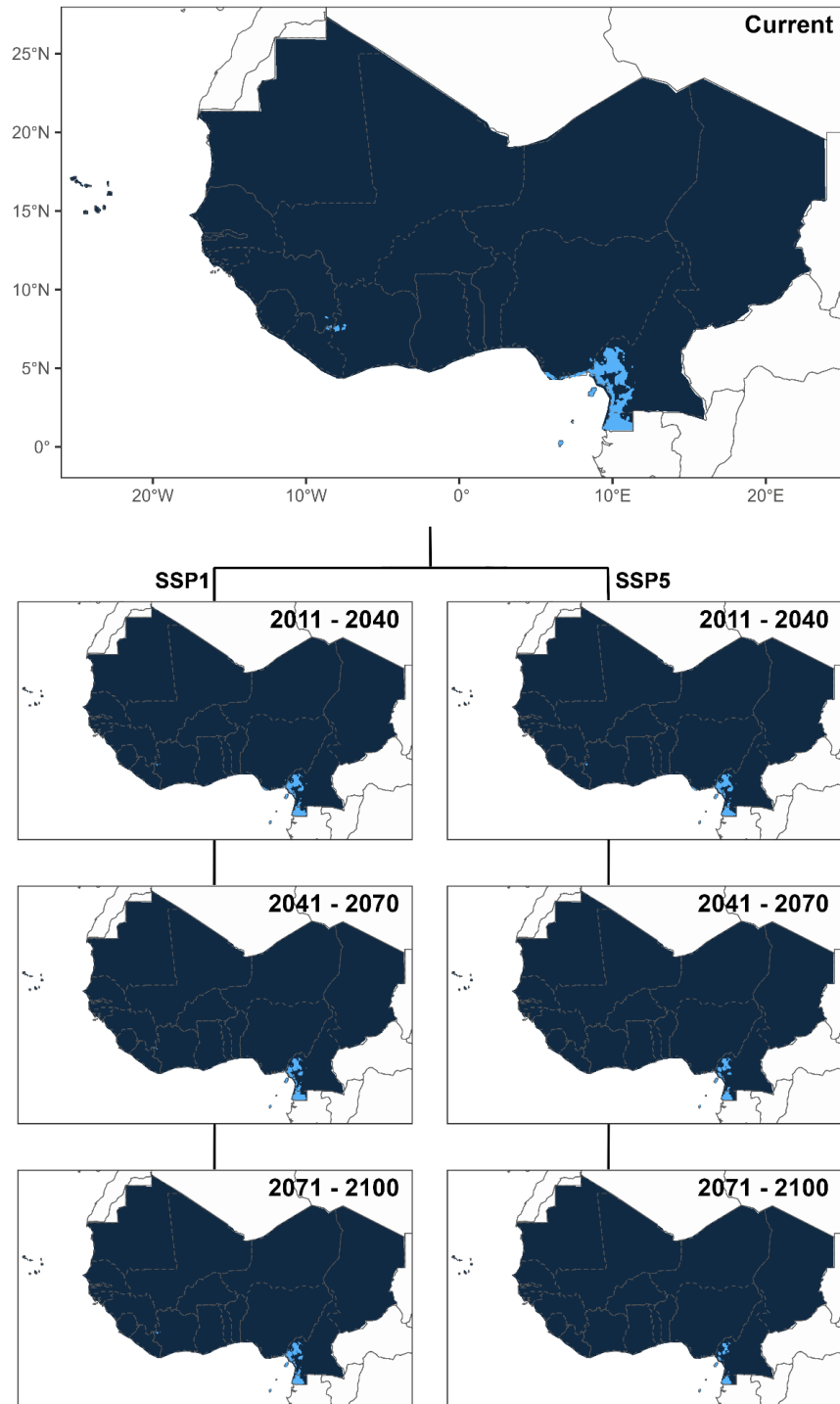


Figure A 20: The distribution hypotheses of *Polyphlebium borbonicum* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

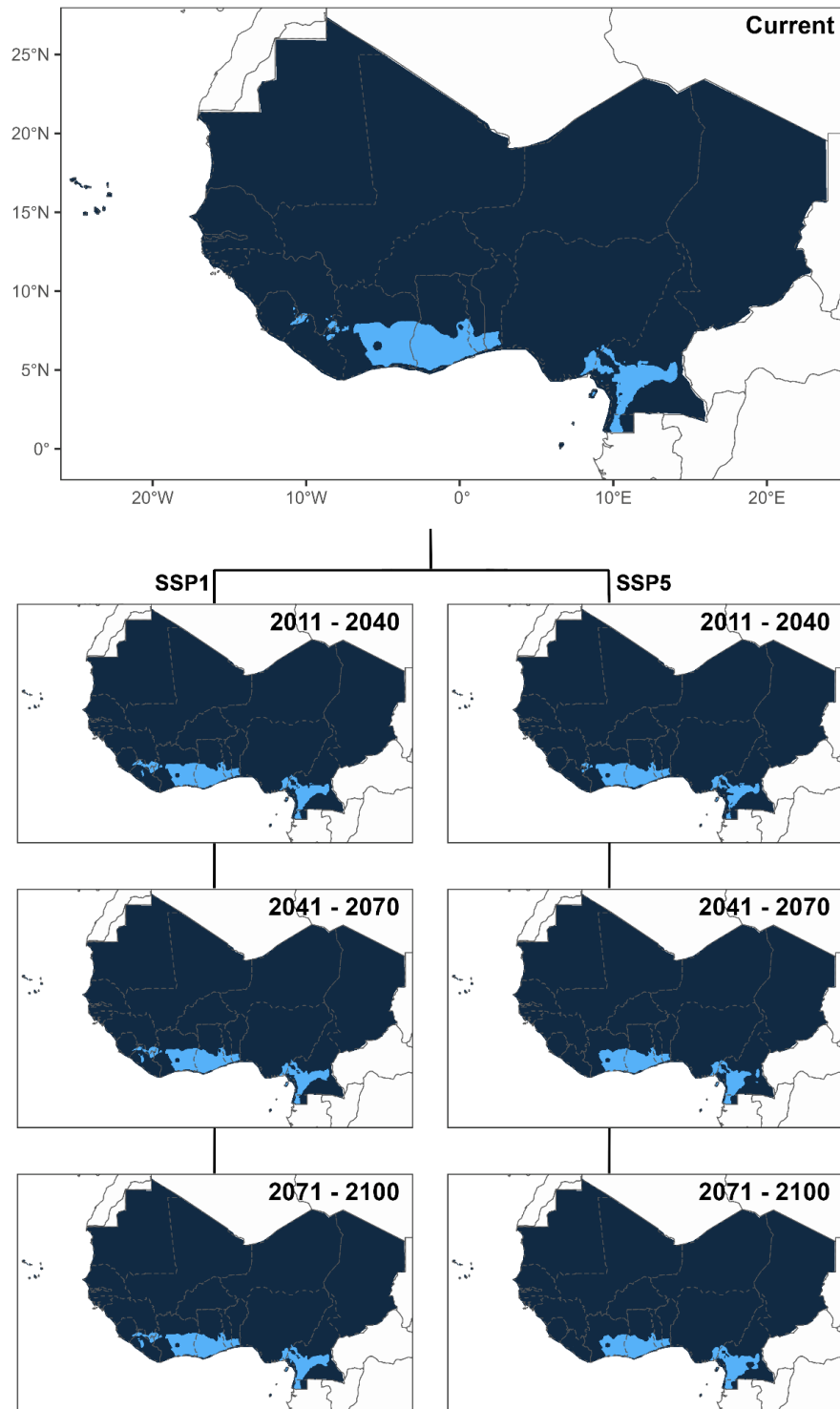


Figure A 21: The distribution hypotheses of *Crepidomanes chevalieri* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

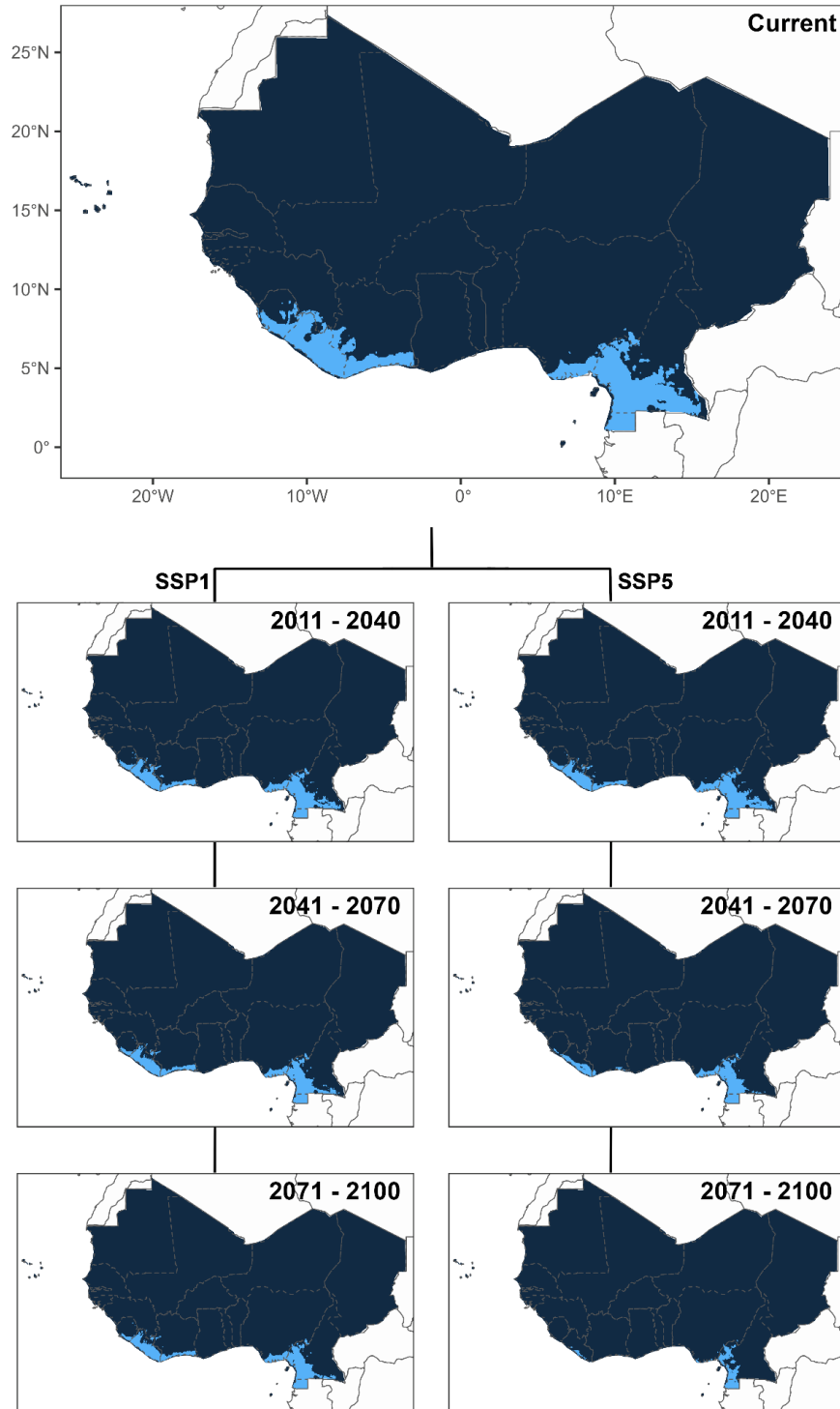


Figure A 22: The distribution hypotheses of *Didymoglossum erosum* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

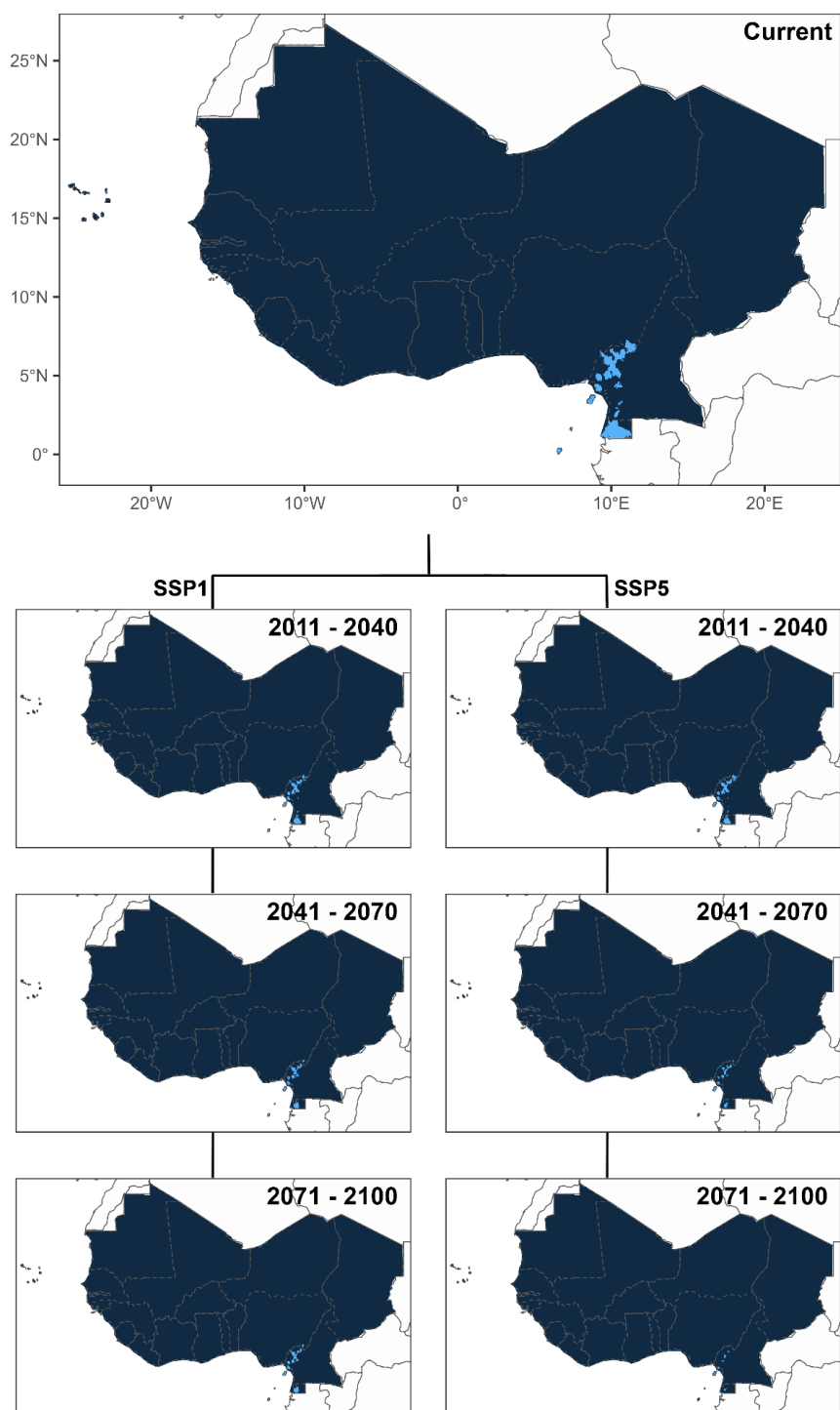


Figure A 23: The distribution hypotheses of *Crepidomanes melanotrichum* (Hymenophyllaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

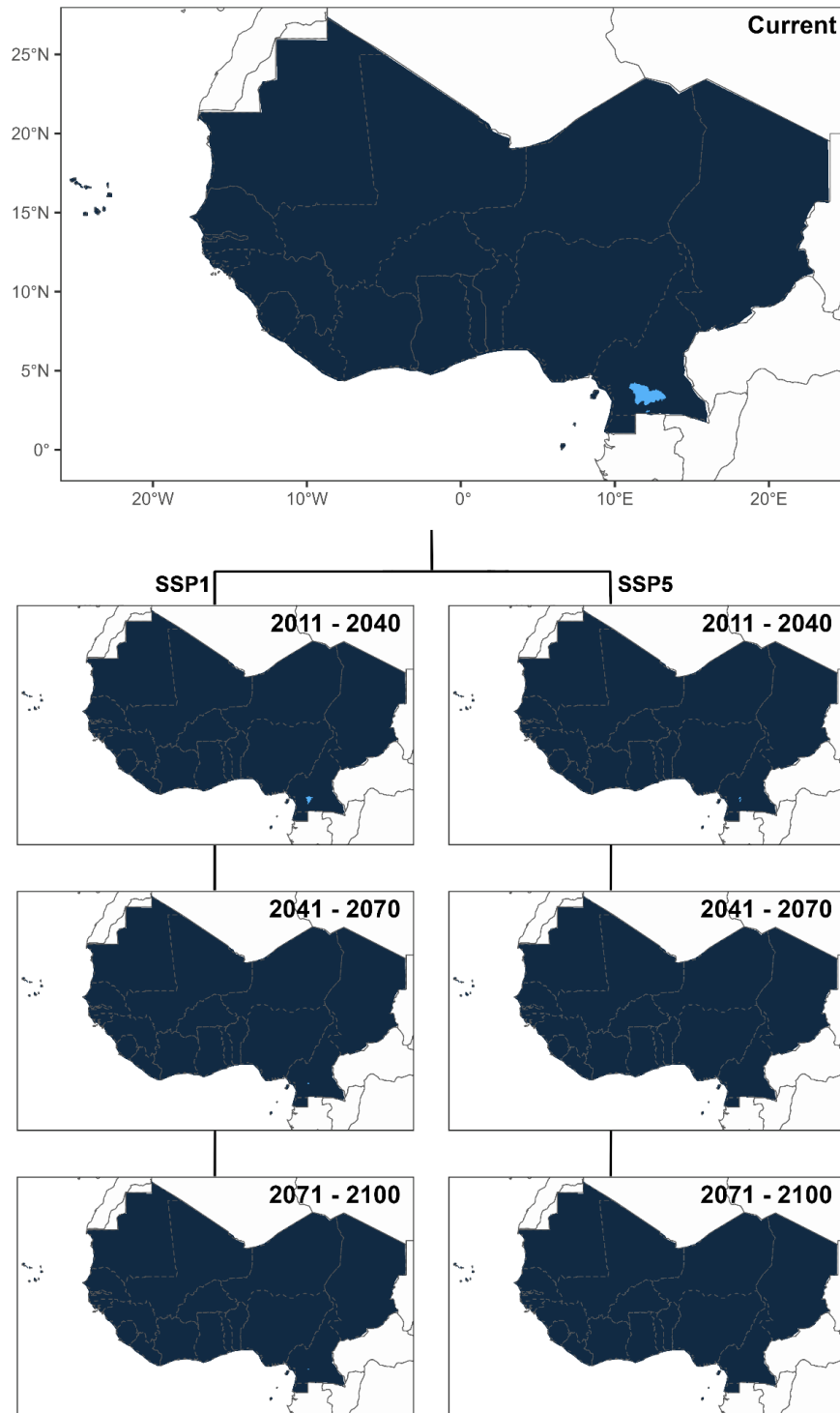


Figure A 24: The distribution hypotheses of *Craterostigma yaundense* (Linderniaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).



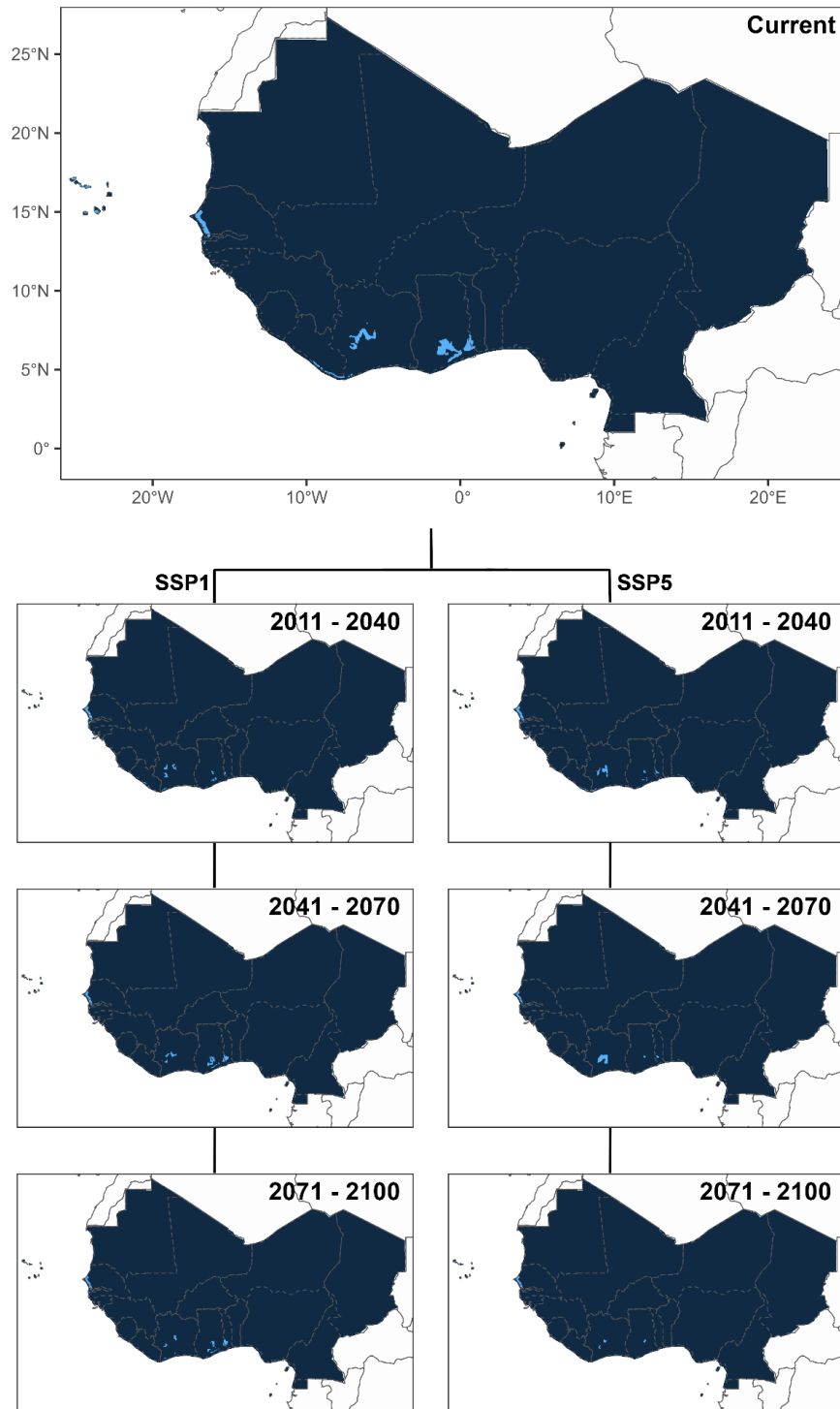


Figure A 25: The distribution hypotheses of *Adiantum incisum* (Pteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

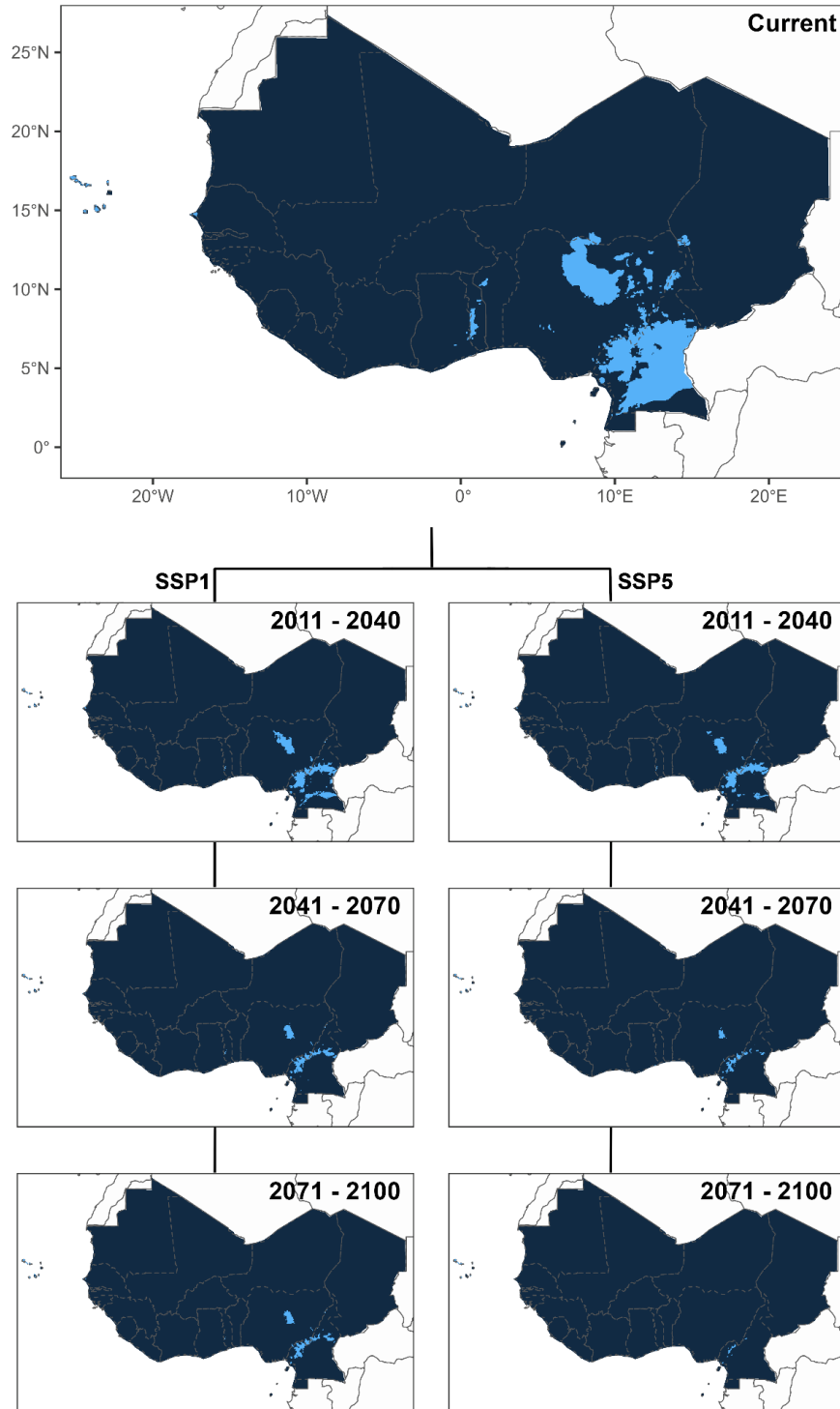


Figure A 26: The distribution hypotheses of *Actiniopteris radiata* (Pteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

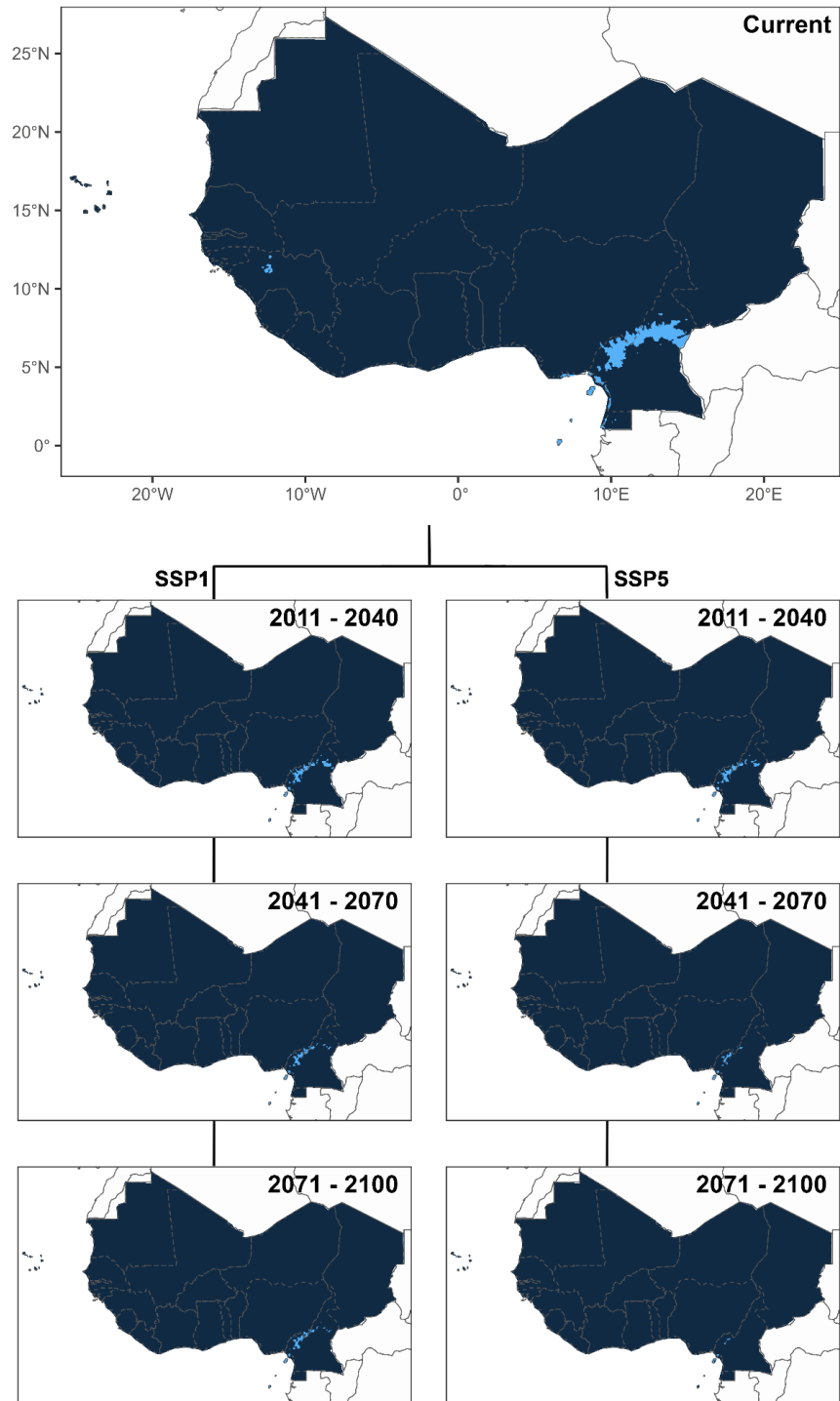


Figure A 27: The distribution hypotheses of *Hemionitis farinosa* (Pteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

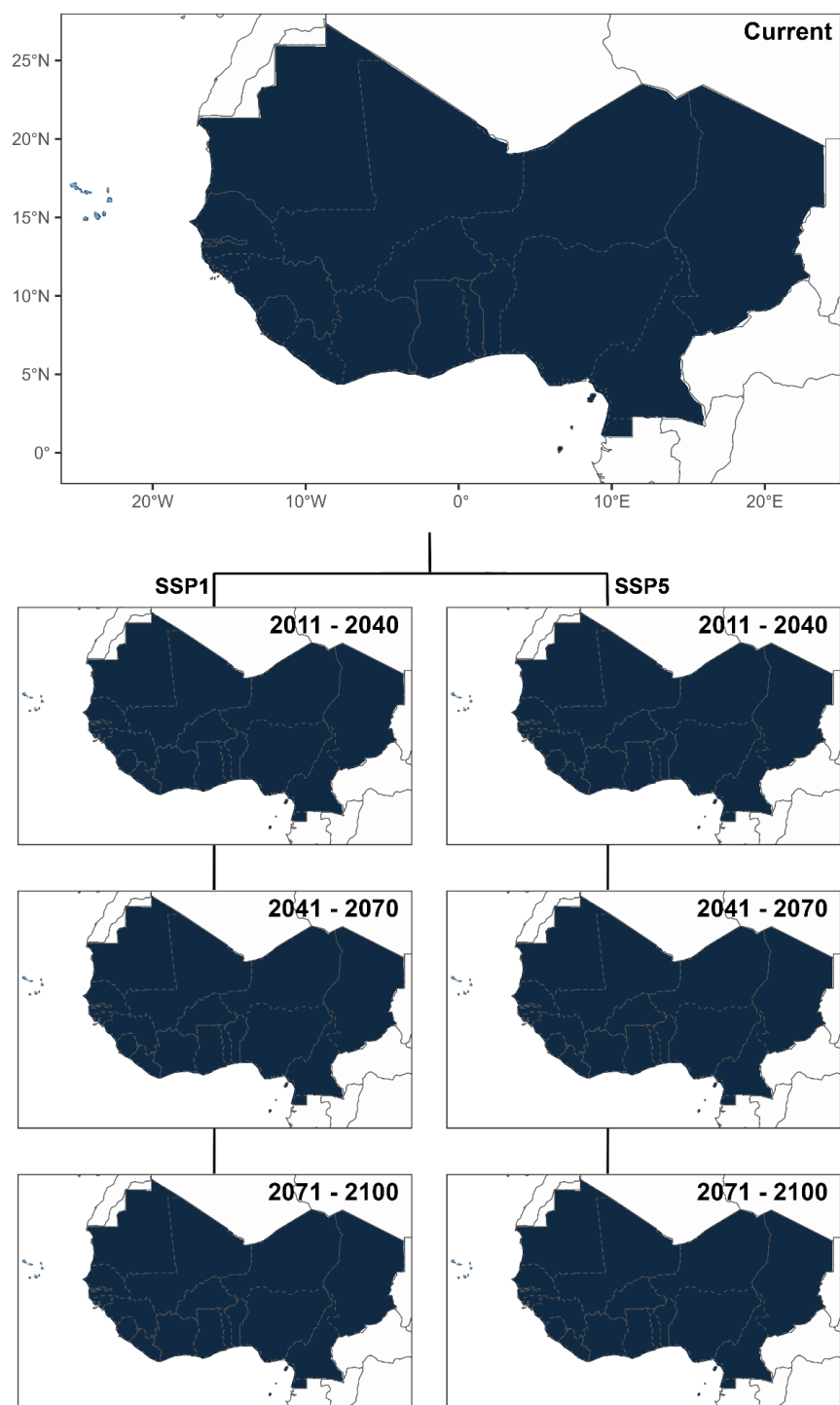


Figure A 28: The distribution hypotheses of *Cosentinia vellea* (Pteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

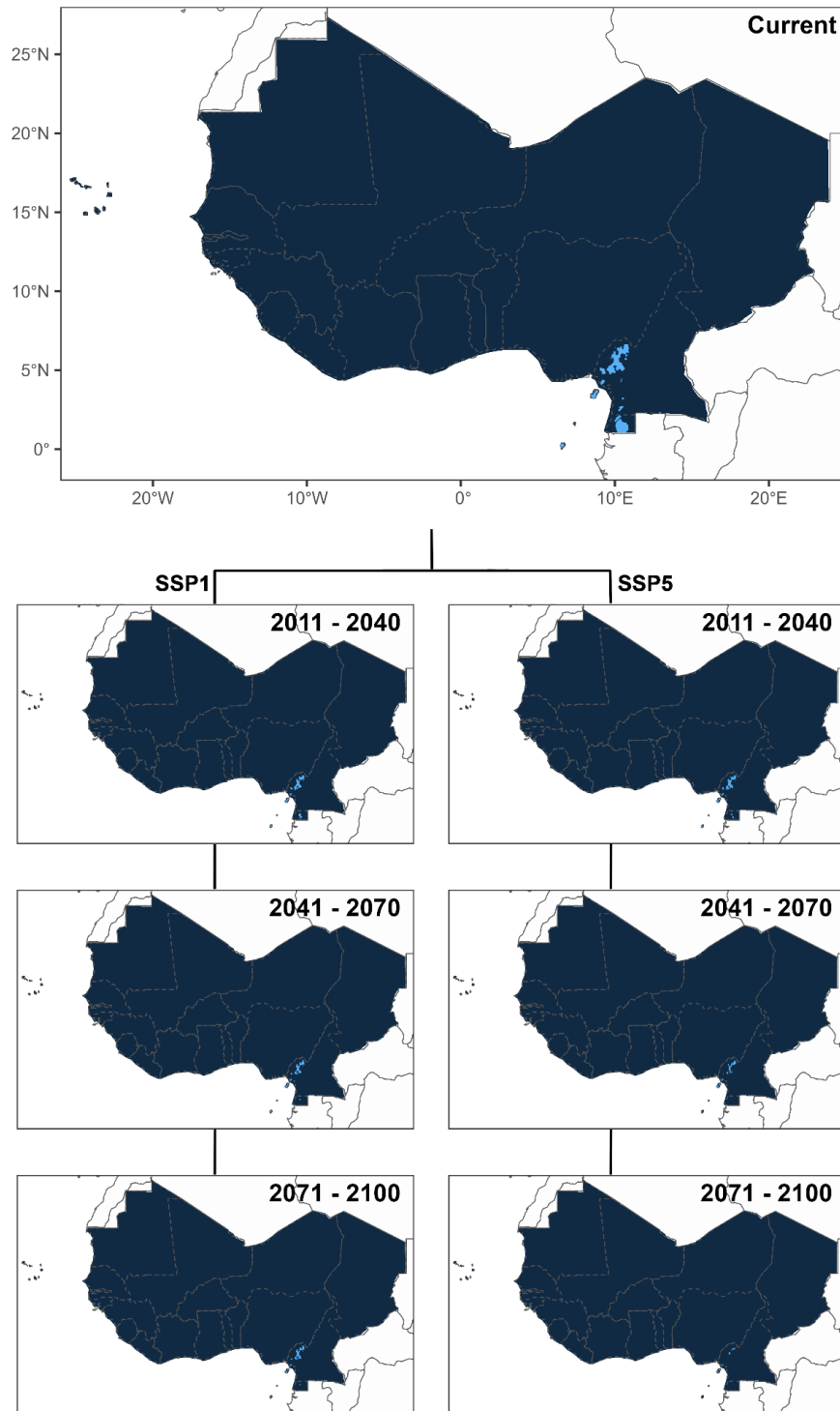


Figure A 29: The distribution hypotheses of *Melpomene flabelliformis* (Polypodiaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

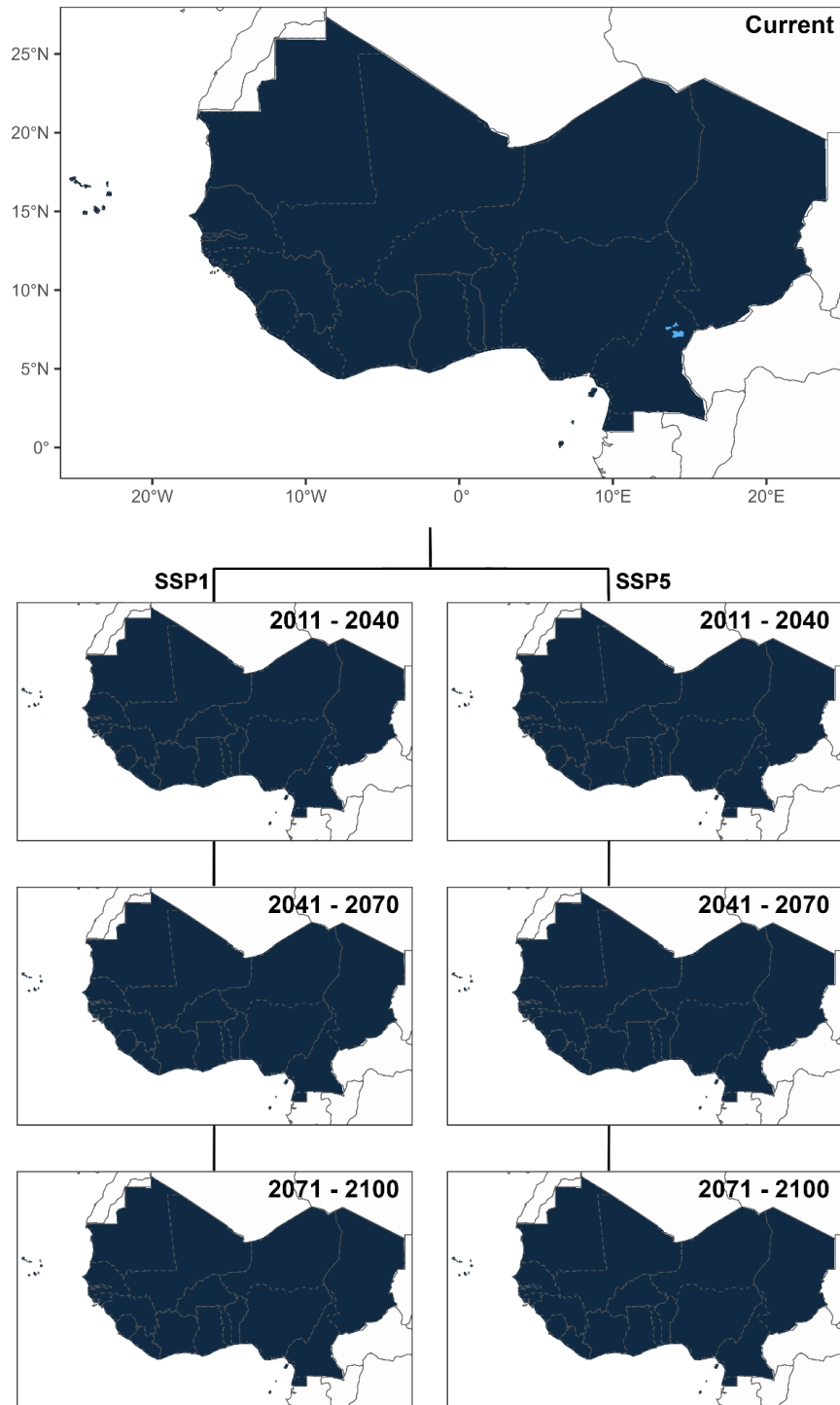


Figure A 30: The distribution hypotheses of *Cheilanthes inaequalis* (Pteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

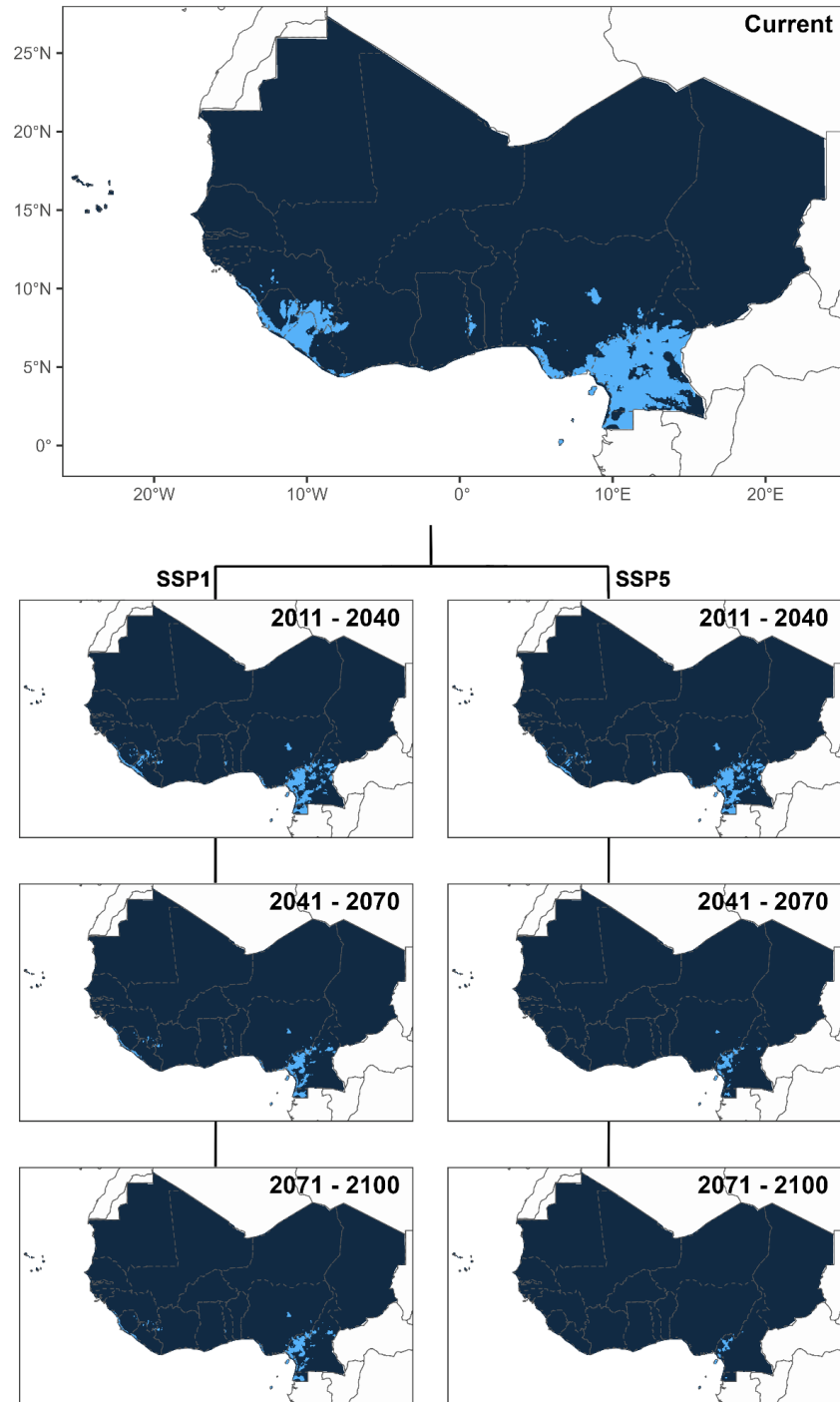


Figure A 31: The distribution hypotheses of *Loxogramme abyssinica* (Polypodiaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

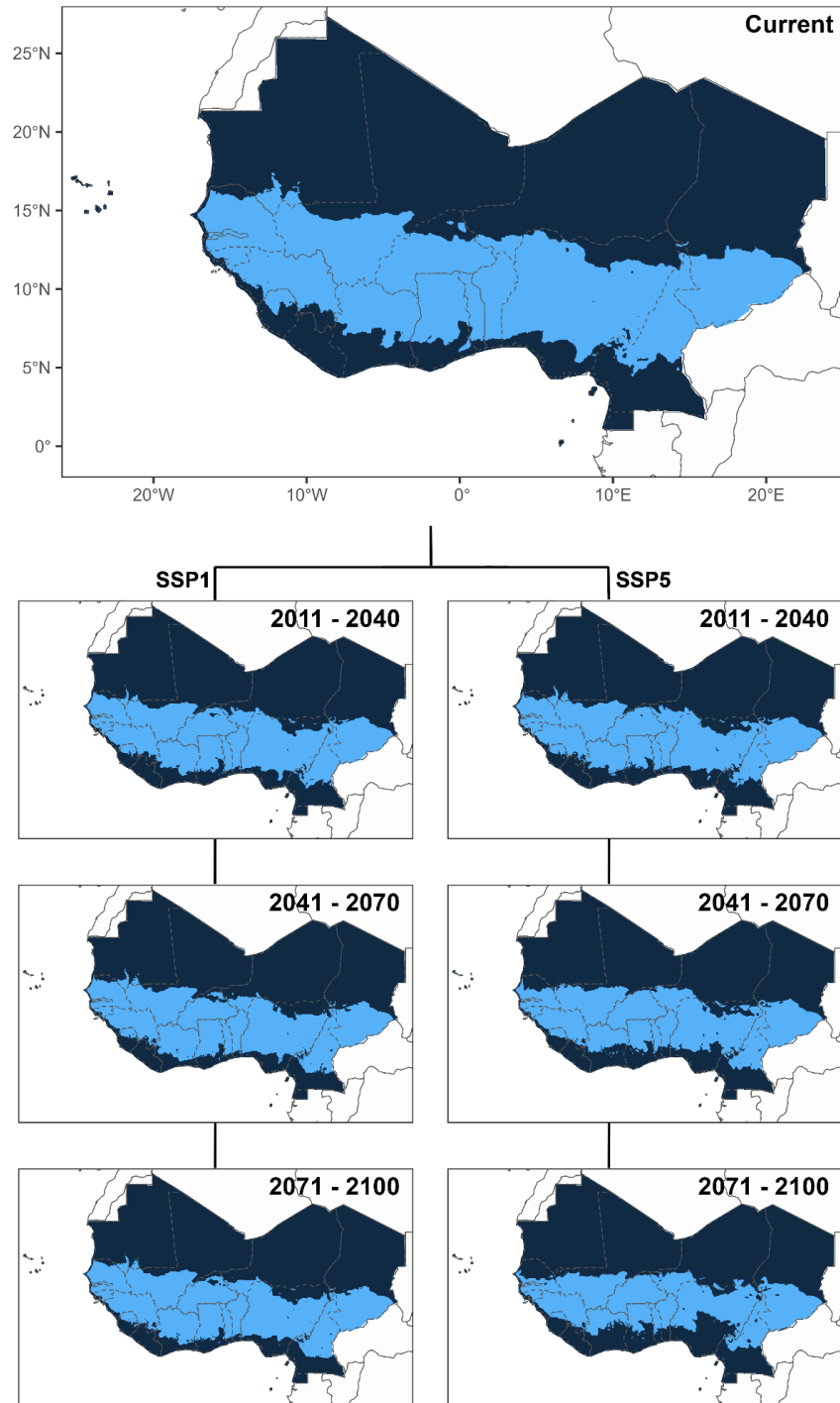


Figure A 32: The distribution hypotheses of *Microchloa indica* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).



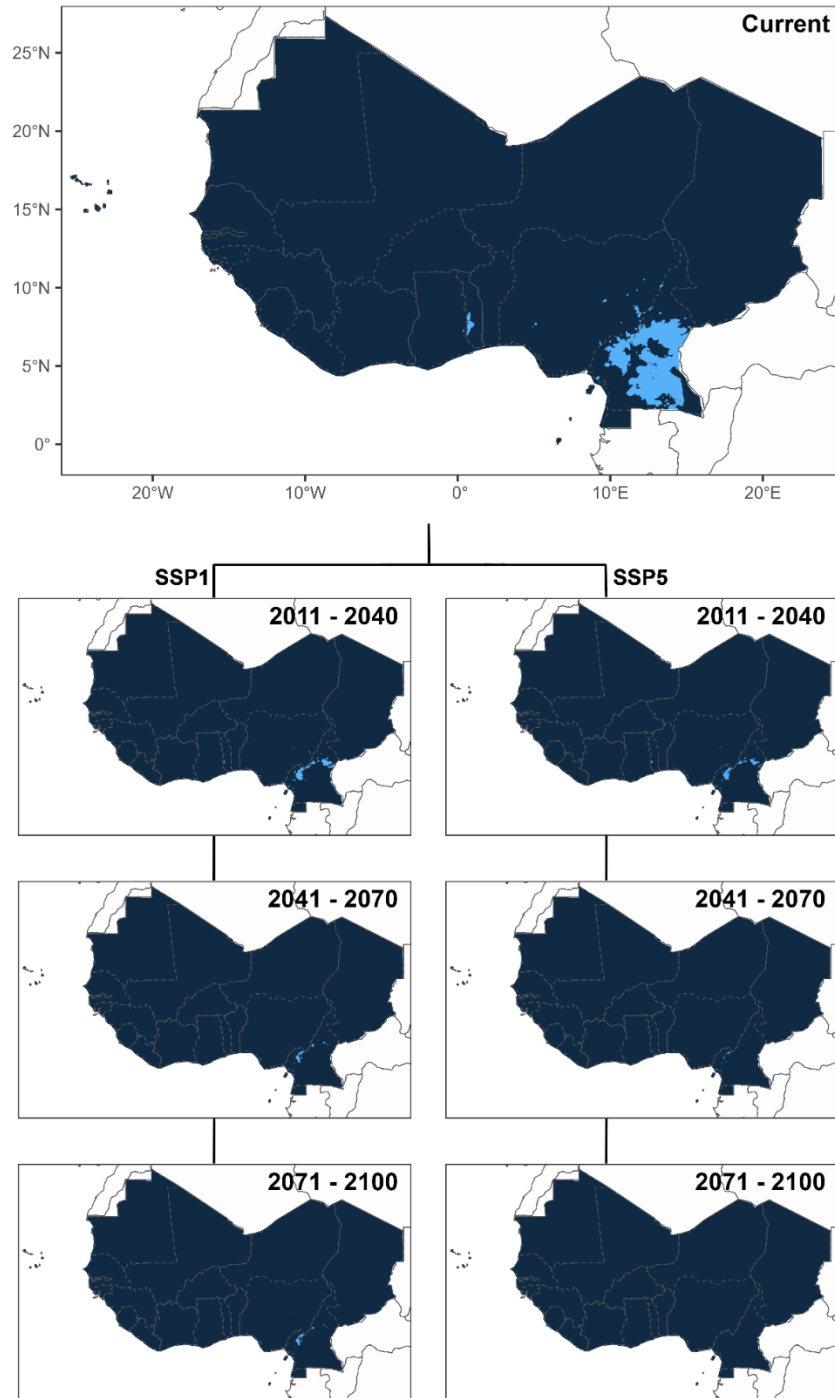


Figure A 33: The distribution hypotheses of *Microchloa kunthii* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

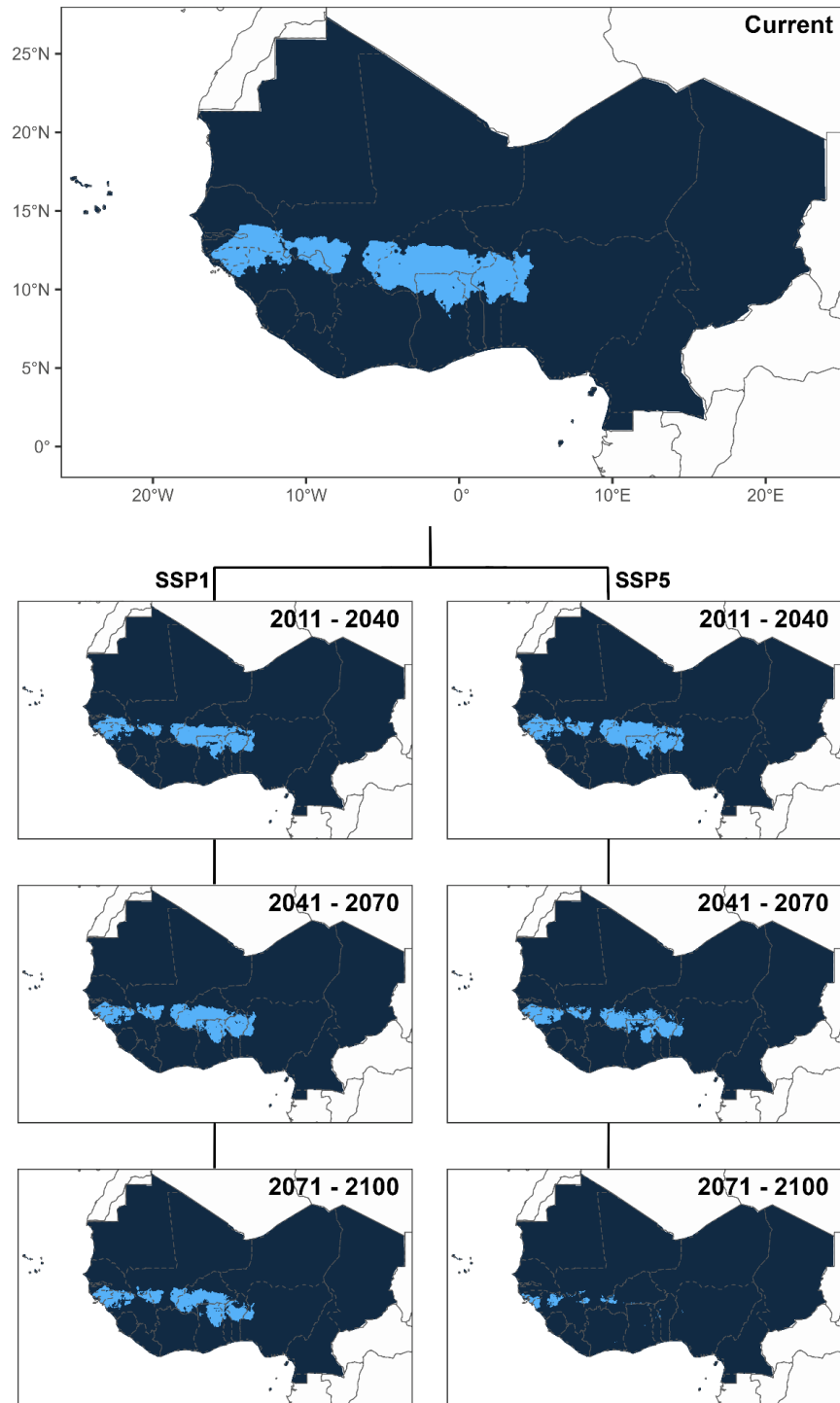


Figure A 34: The distribution hypotheses of *Oropetium aristatum* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

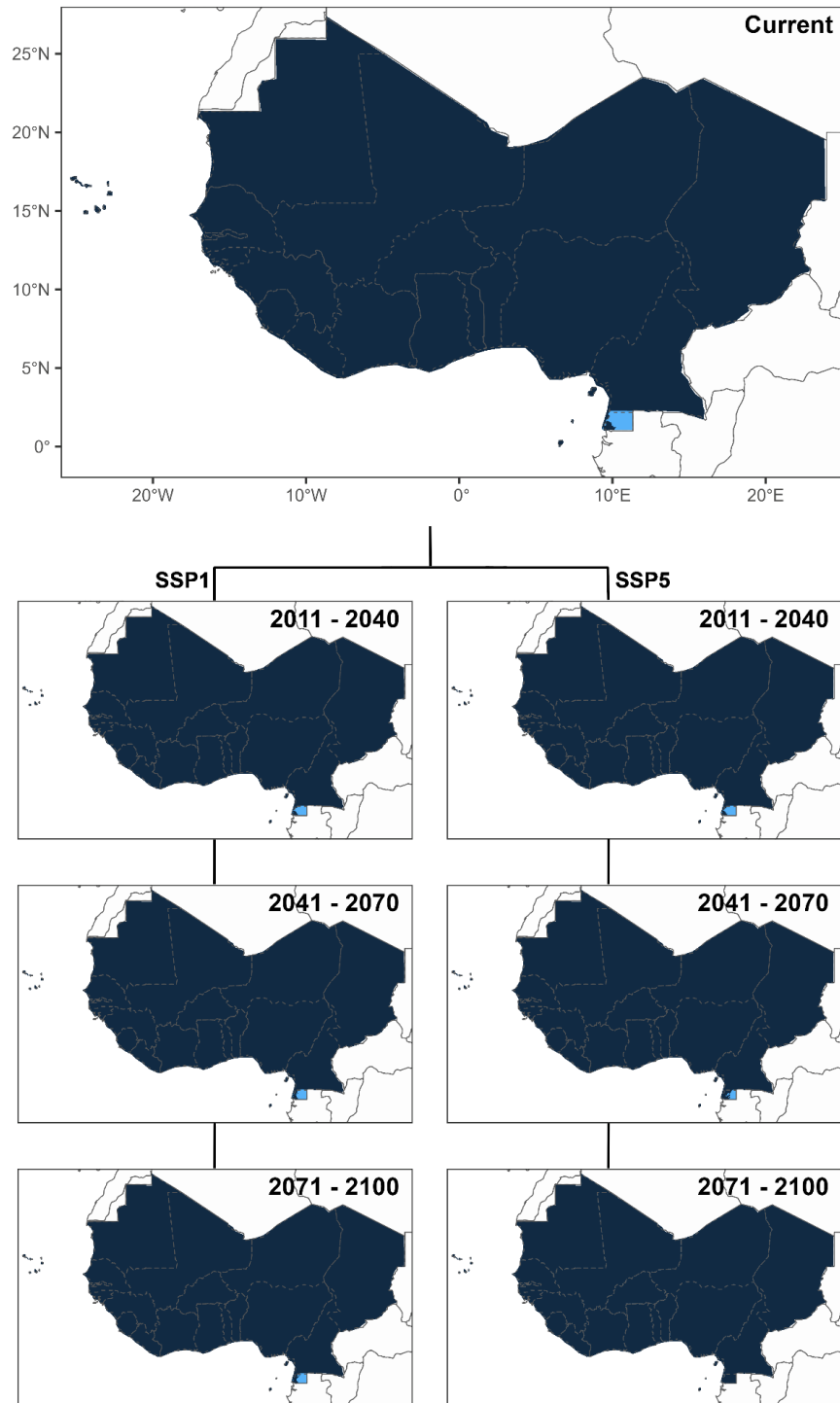


Figure A 35: The distribution hypotheses of *Pellaea dura* (Pteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

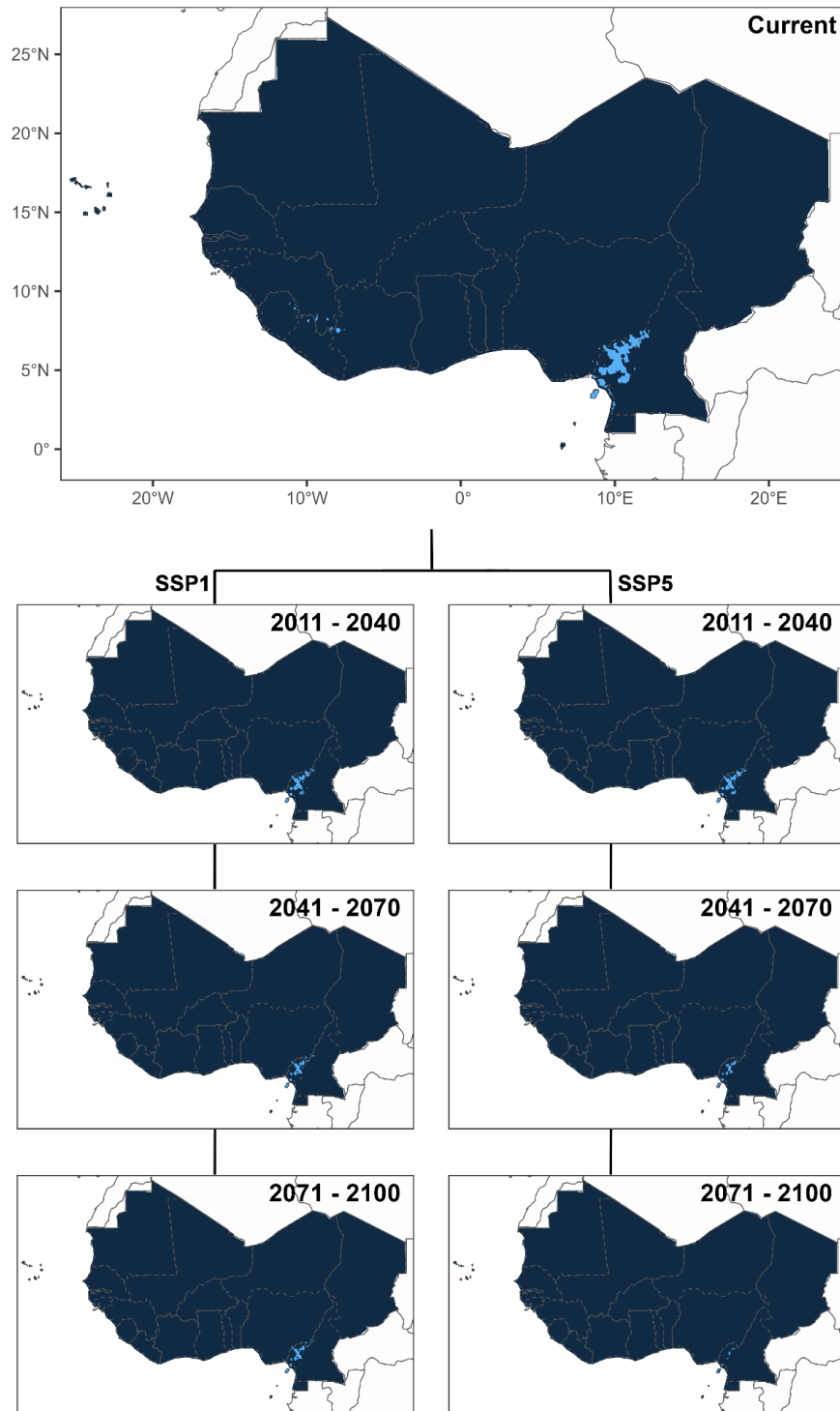


Figure A 36: The distribution hypotheses of *Pleopeltis macrocarpa* (Polypodiaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

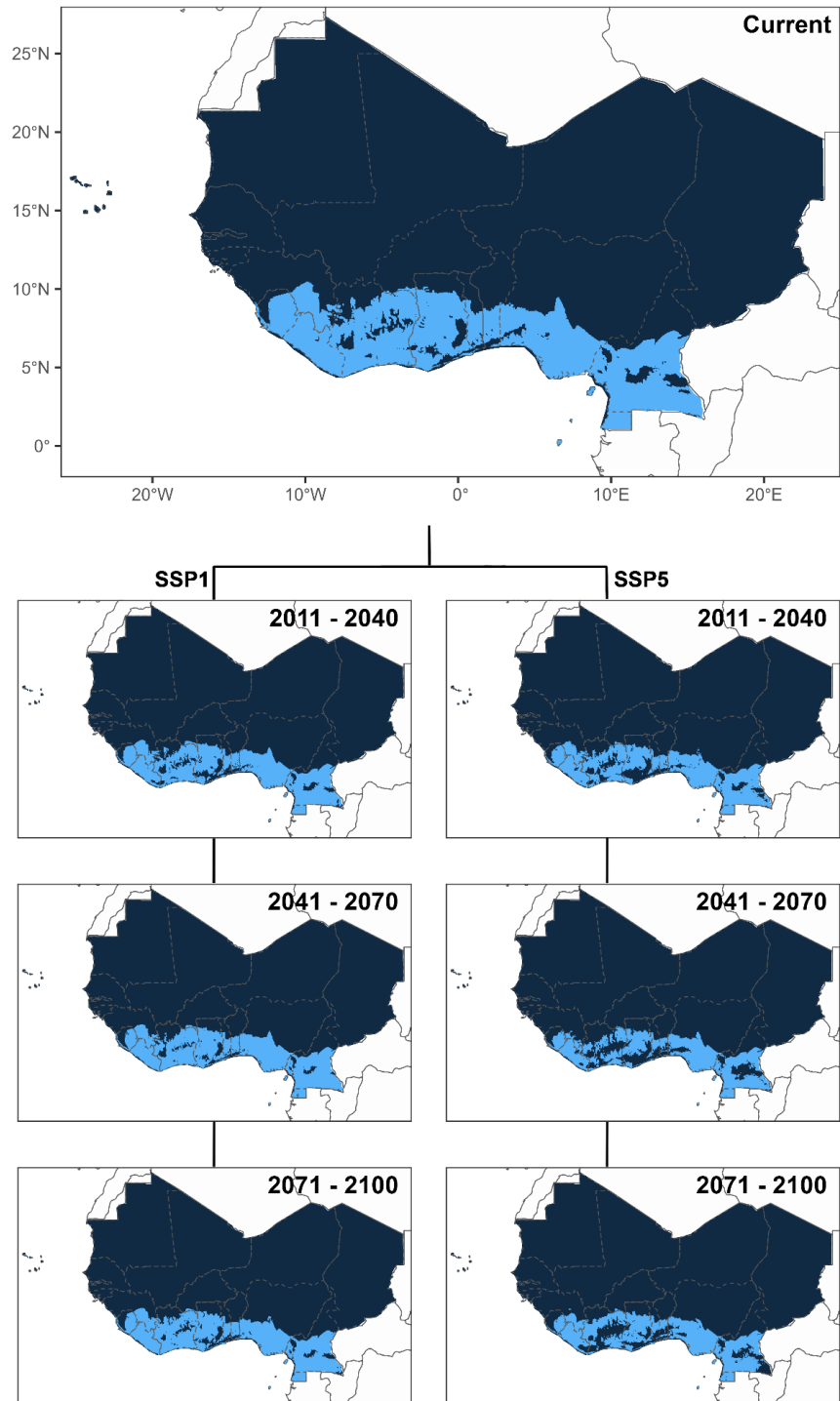


Figure A 37: The distribution hypotheses of *Phymatosorus scolopendria* (Polypodiaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

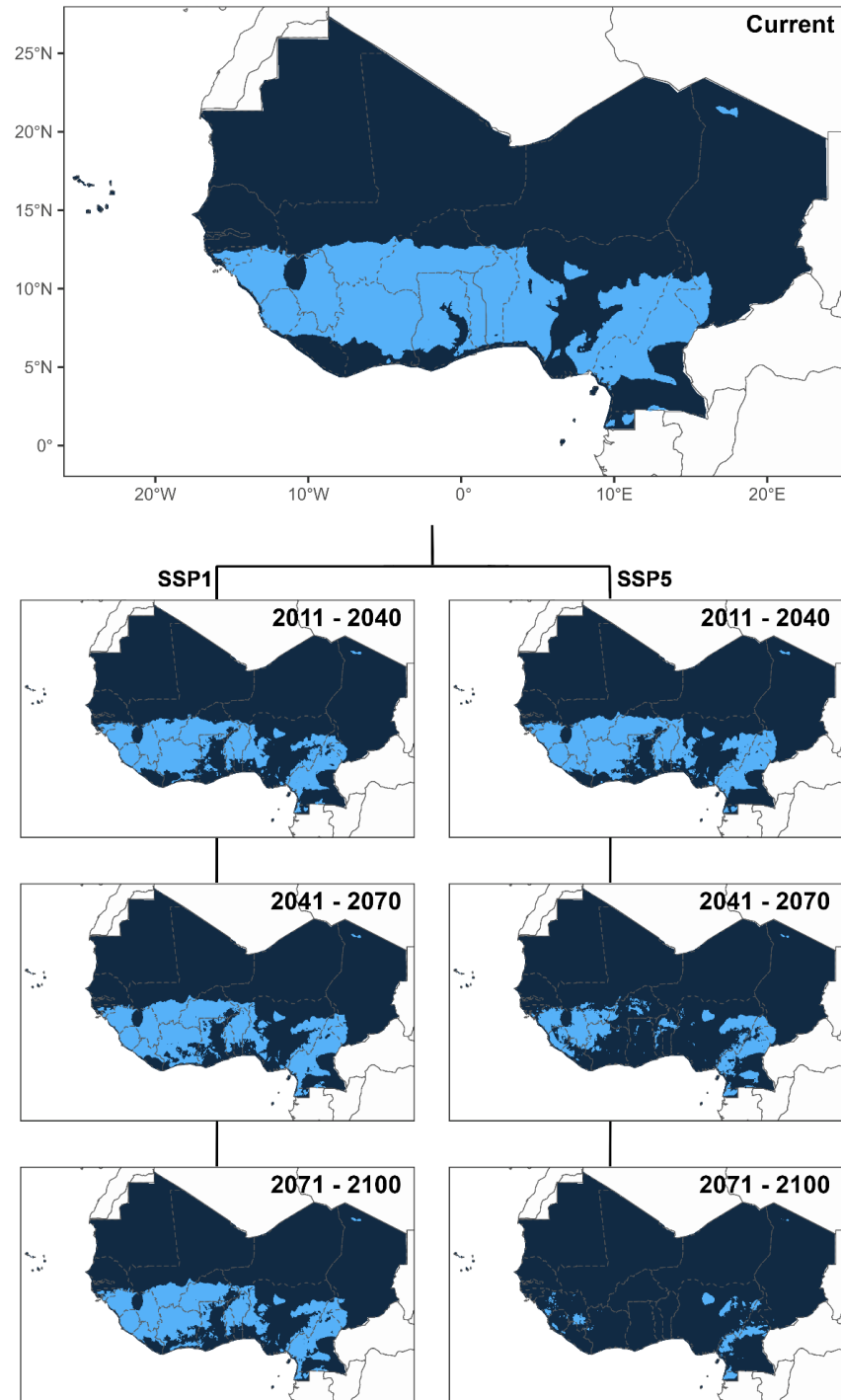


Figure A 38: The distribution hypotheses of *Sporobolus festivus* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

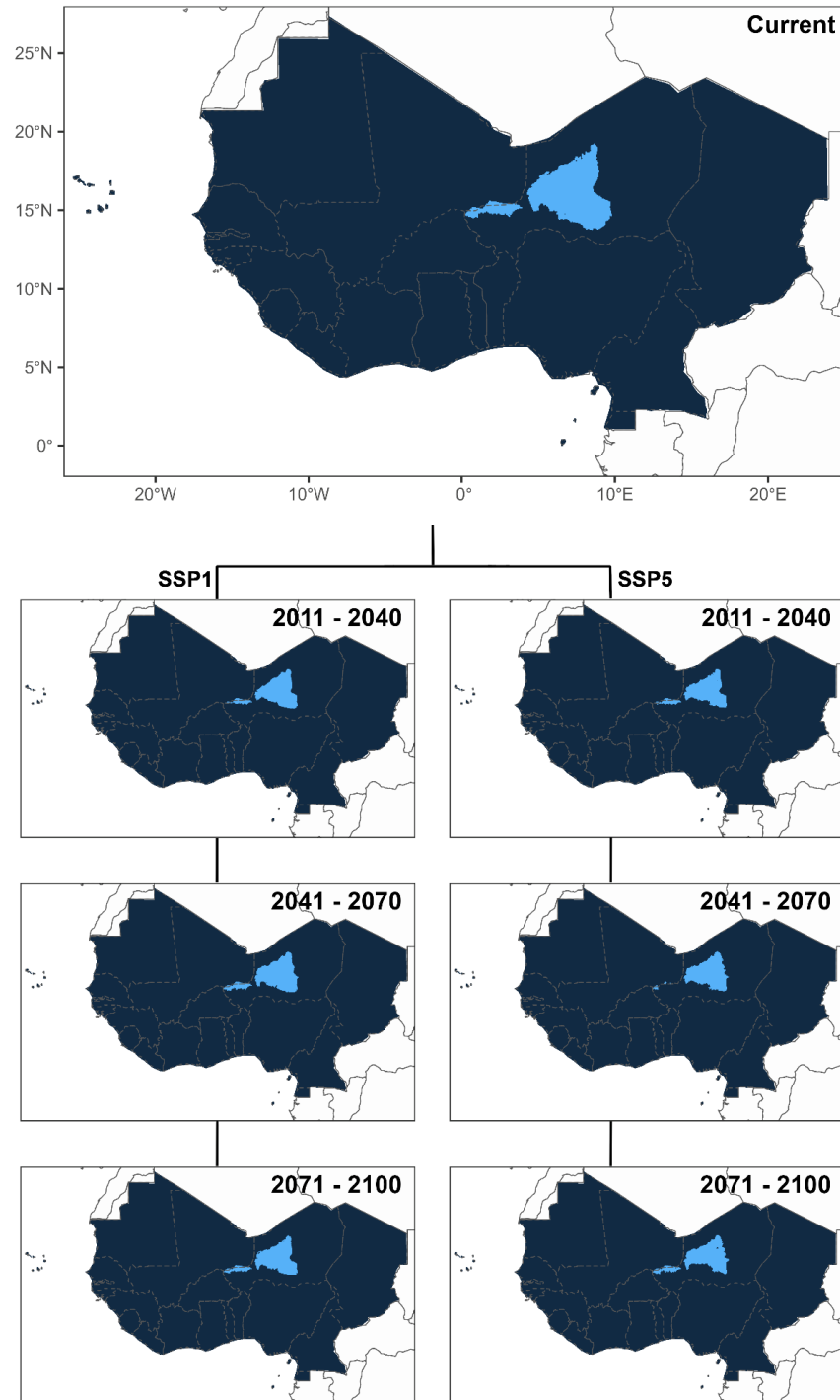


Figure A 39: The distribution hypotheses of *Sporobolus pellucidus* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

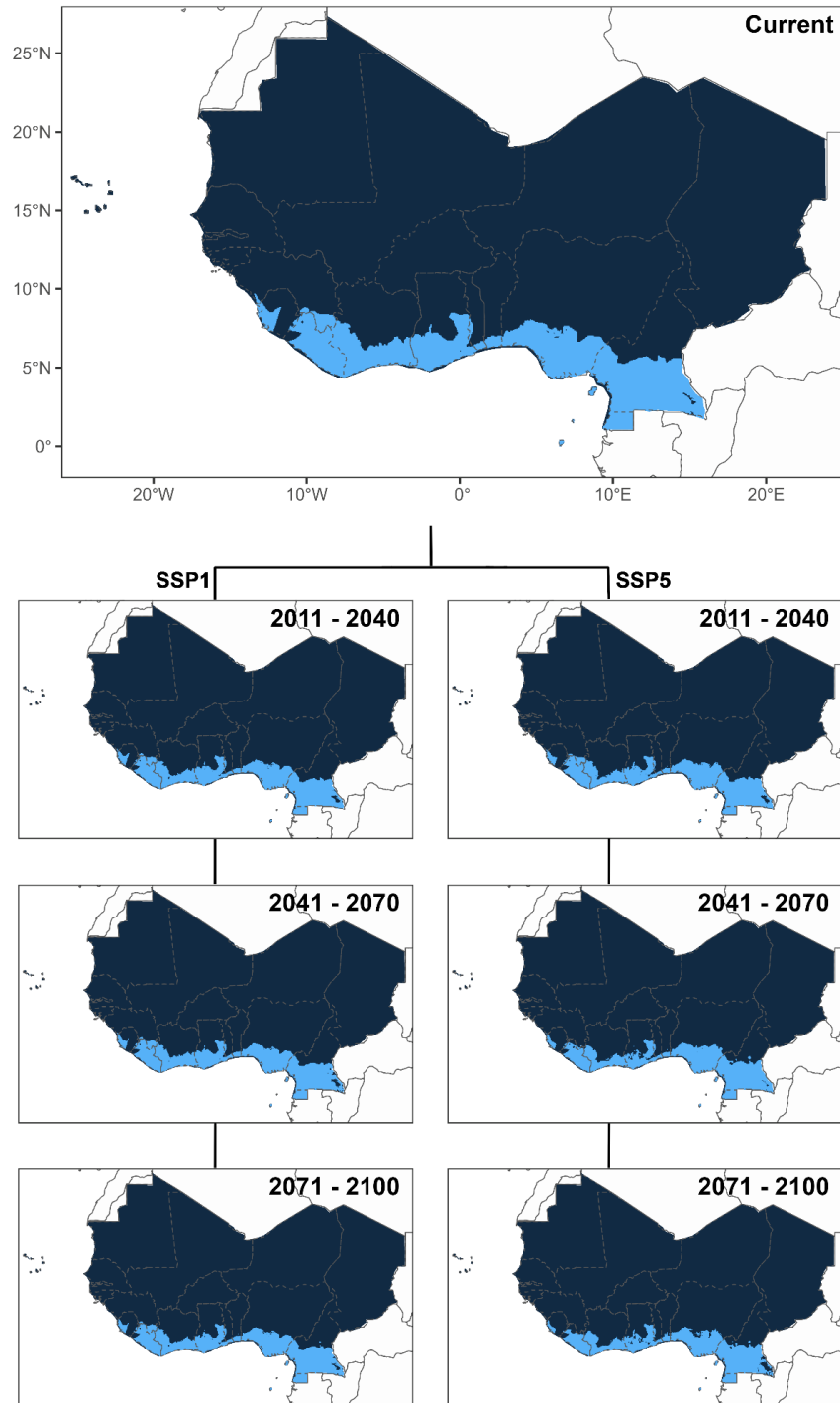


Figure A 40: The distribution hypotheses of *Platycerium stemaria* (Polypodiaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).



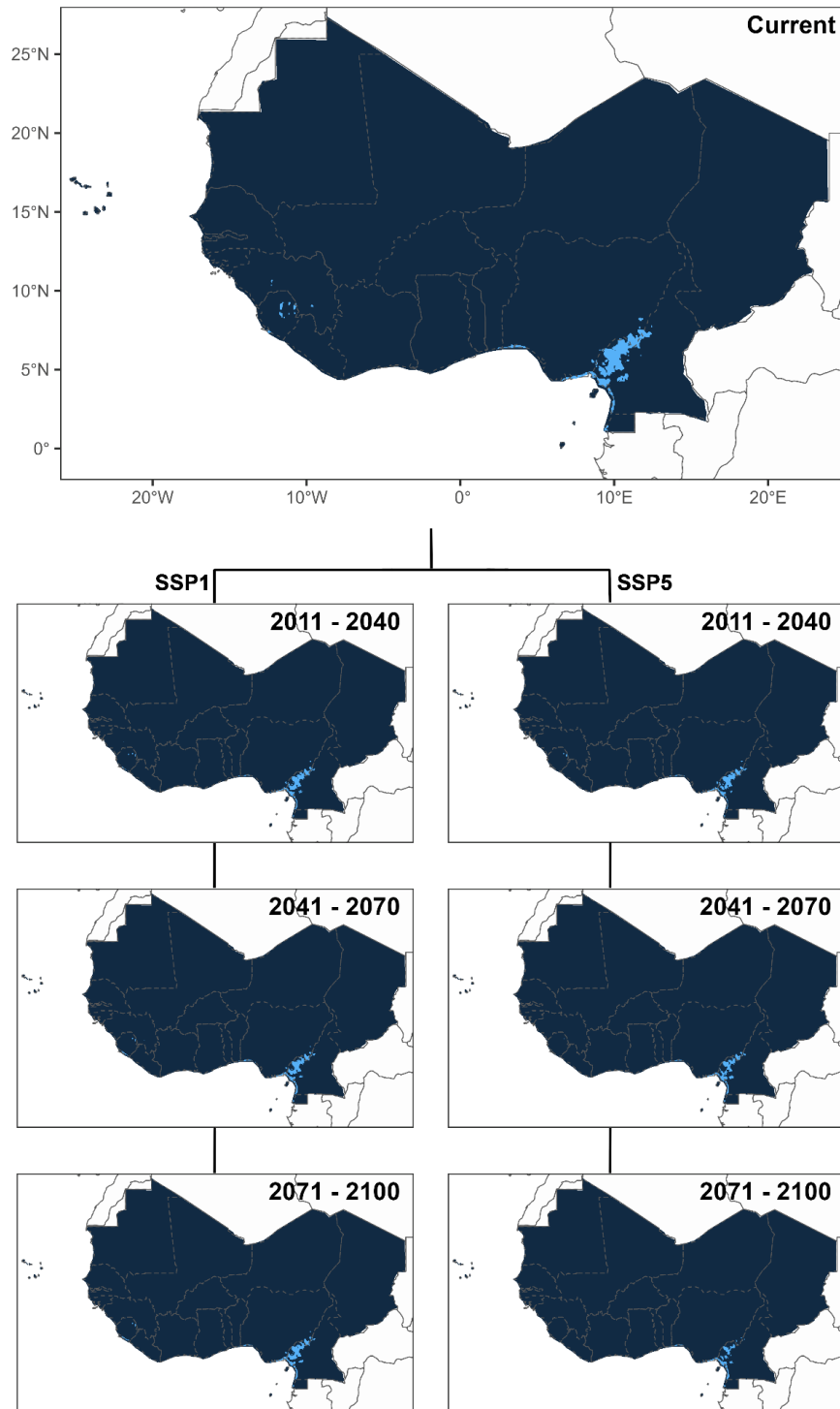


Figure A 41: The distribution hypotheses of *Tripogon major* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

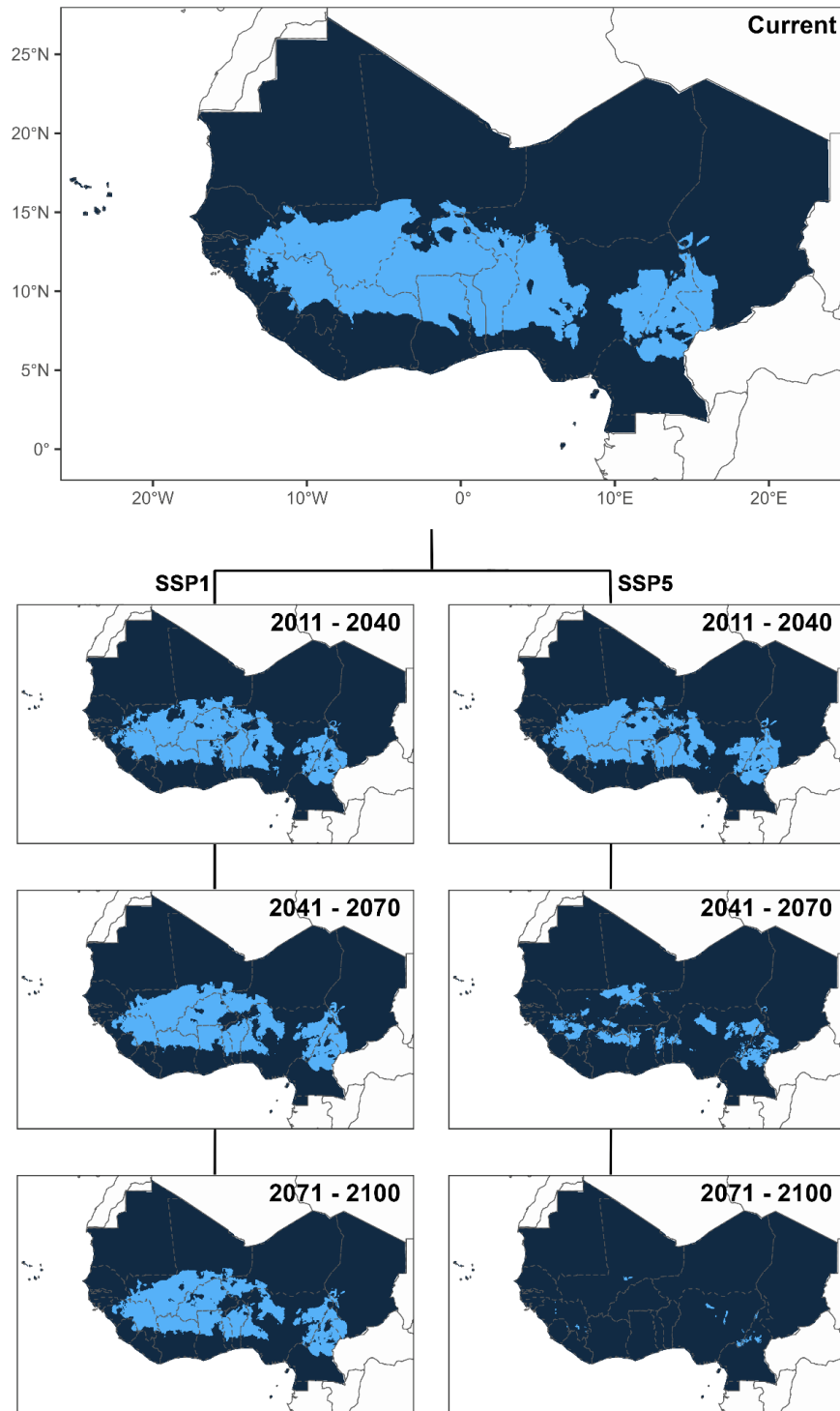


Figure A 42: The distribution hypotheses of *Tripogonella minima* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

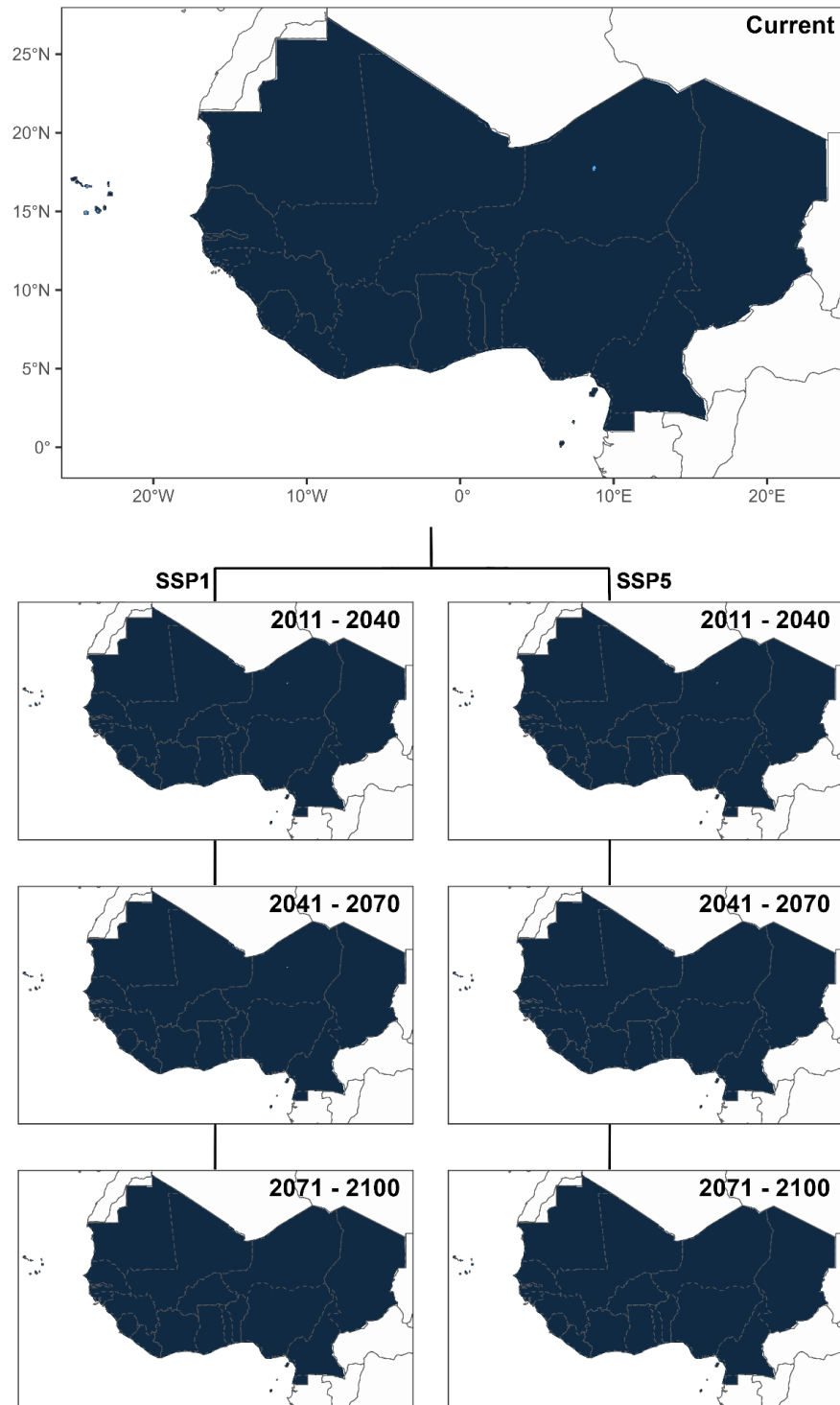


Figure A 43: The distribution hypotheses of *Tripogon multiflorus* (Poaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

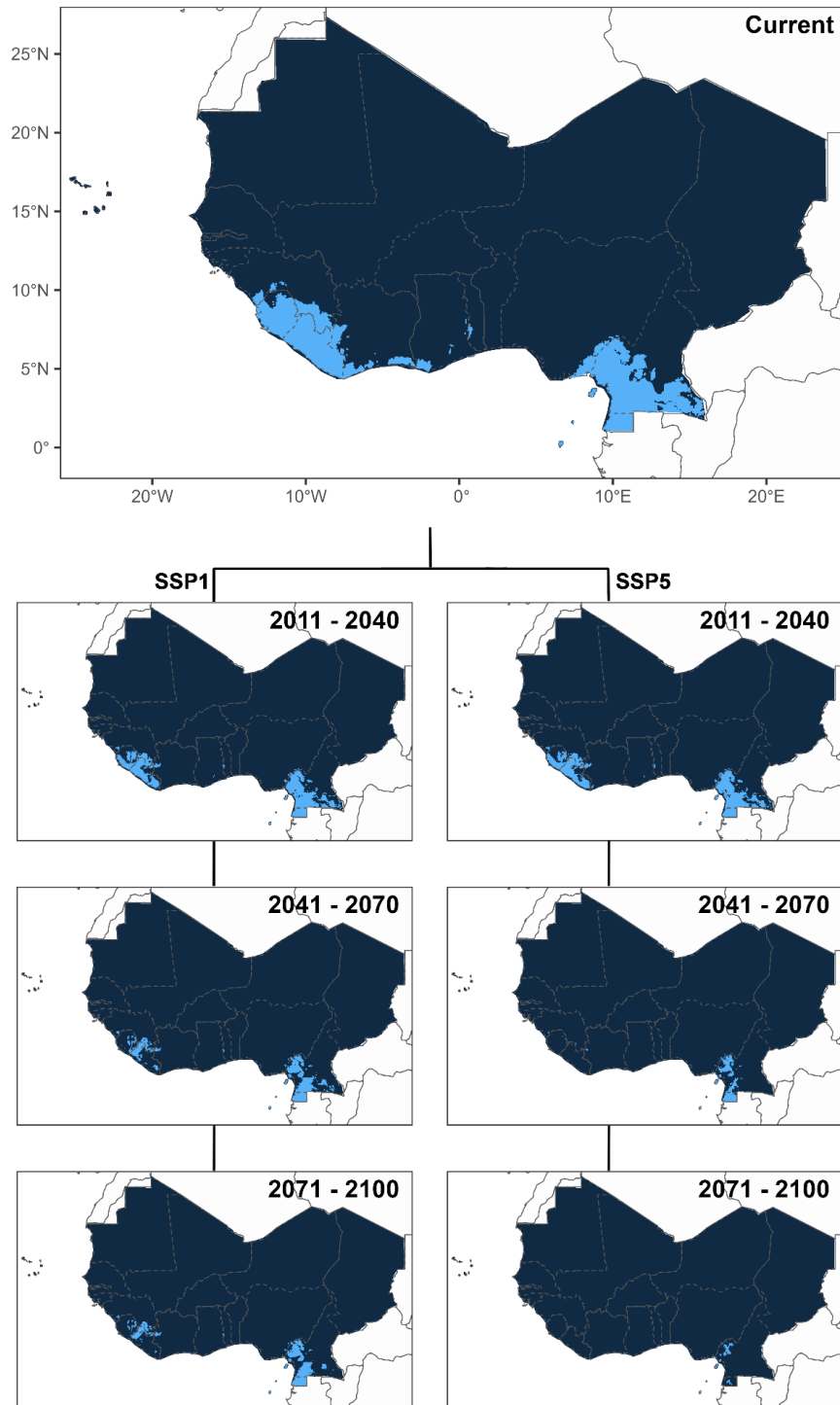


Figure A 44: The distribution hypotheses of *Vittaria guineensis* (Pteridaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

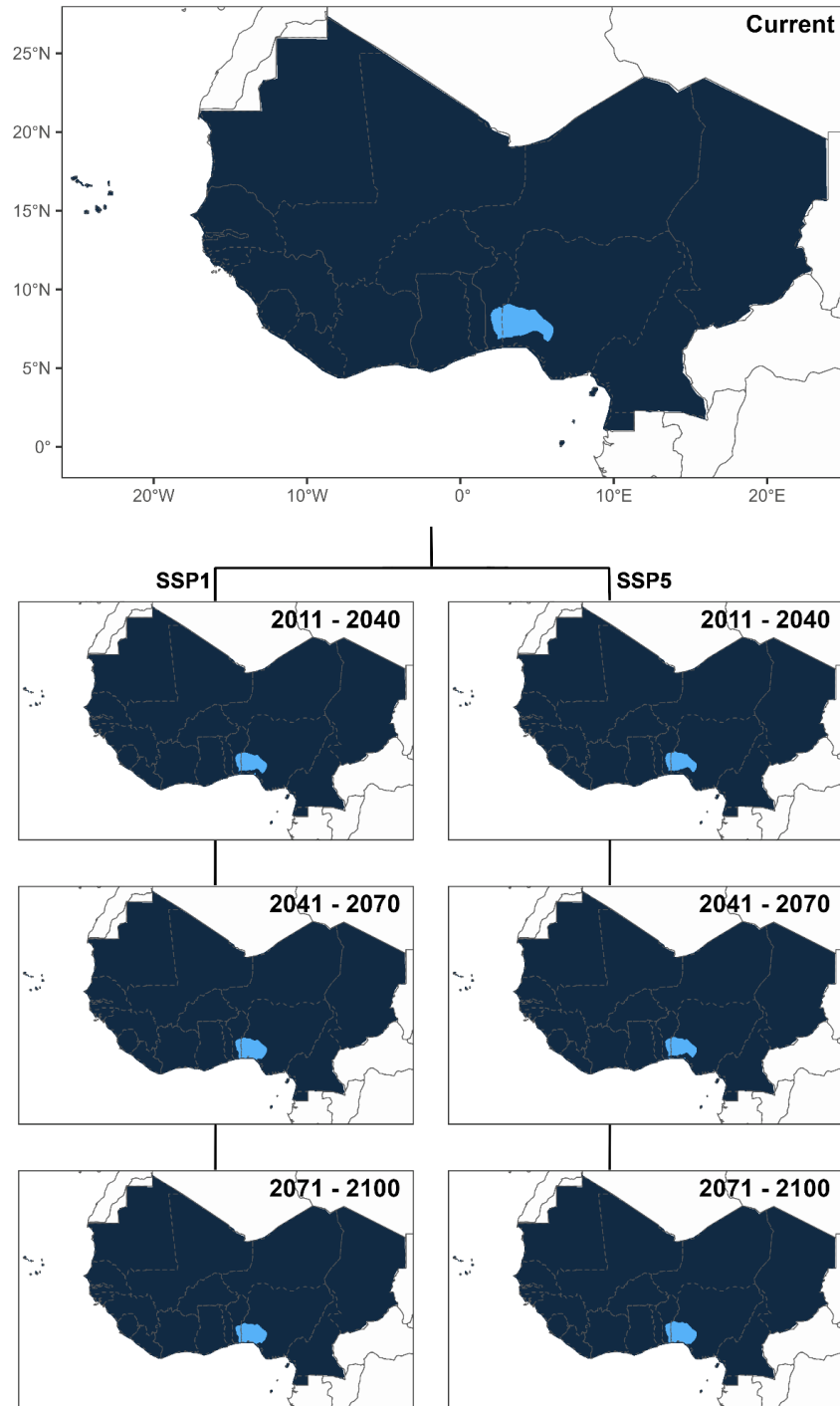


Figure A 45: The distribution hypotheses of *Selaginella njamnjamensis* (Selaginellaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

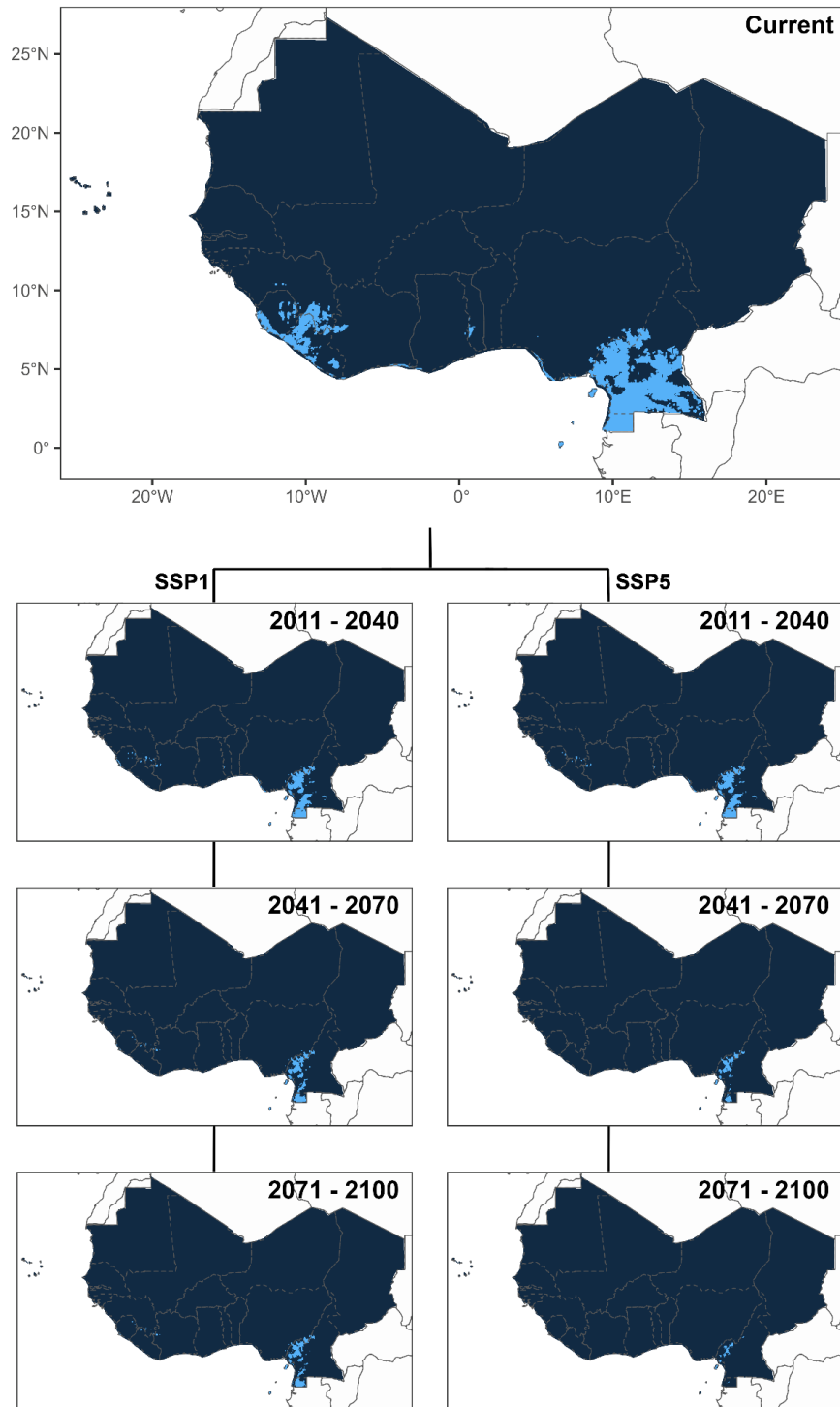


Figure A 46: The distribution hypotheses of *Arthropteris orientalis* (Tectariaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

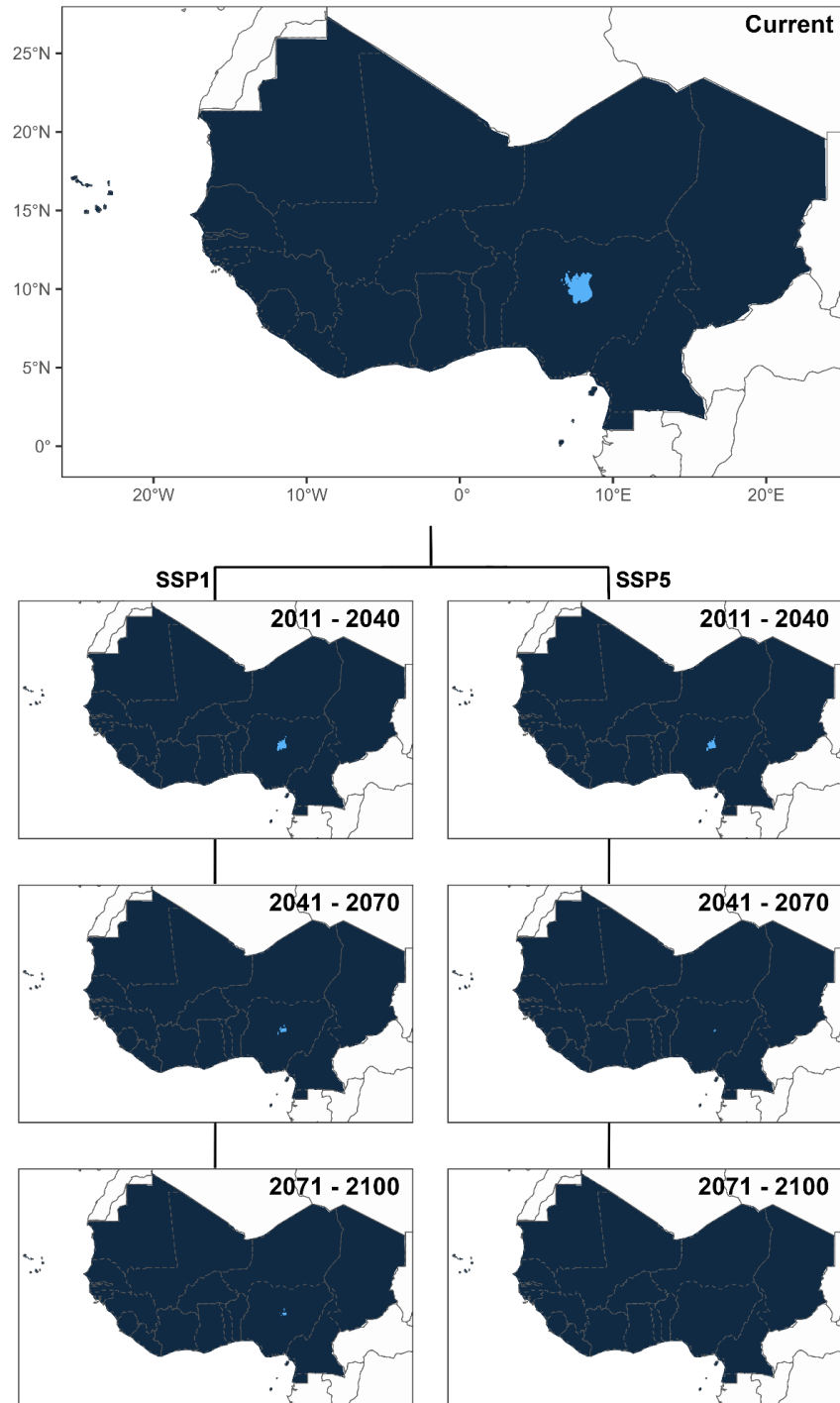


Figure A 47: The distribution hypotheses of *Xerophyta schnizleinia* (Velloziaceae) in the present and under different climate change scenarios (the most sustainable shared socioeconomic pathway, SSP1, and the fossil-fuel-intensive shared socioeconomic pathway, SSP5) and across different time-series (2011-2040, 2041-2070, and 2071-2100).

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## **PUBLICATION**

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## Article

# Desiccation-Tolerant Vascular Plants: A Group of Species Largely Neglected in Conservation

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## Abstract

The anthropogenic drivers of biodiversity loss are causing a global decline in biodiversity, yet some species remain overlooked in conservation efforts. In this study, we address the gaps between the current discussions and pressing issues on these species' conservation. We focused on West Africa and used desiccation-tolerant vascular plants to conduct a systematic review of conservation discussions and a study case to assess their protection and exposure to quarrying and climate change. Our systematic review revealed, for the first time, that these plants are largely neglected in conservation discussions. Most species lack formal evaluations, and only four studies mentioned conservation, although without providing enough evidence to justify it. In our case study, we found biased protection among the species, with varying effectiveness of the protection areas against different anthropogenic threats. The two most exposed species were not present in protected areas, which were more effective at mitigating quarrying impacts than climate change. We highlight the need for conservation-explicit assessments and a mechanistic understanding of species' conservation needs, such as quantitatively evaluating species vulnerability to threats, to support efficient conservation strategies. We call for conservation initiatives with specific objectives to include overlooked species in protected areas and adjust the conservation objectives to address specific threats.

**Keywords:** climate change; conservation; desiccation tolerance; diversity; land use change; protection areas; quarrying; resurrection plants; rock outcrops



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## 1. Introduction

The world is experiencing high rates of biodiversity loss promoted by human activities [1–3]. However, drawing up global strategies for biodiversity conservation has been a challenging task because the anthropogenic drivers of biodiversity loss operate in different ways and species can be subjected to multiple drivers of strong intensities [1,4]. For example, land use change is mostly promoted by direct and local interventions on natural systems. On the other hand, climate change is indirectly triggered by global human activities, with some locations more exposed to changes regardless of their origin [5]. The intensity of both land use change and climate change is rising in some regions of the world such as West Africa [6,7], which includes areas recognized as global biodiversity hotspots [8]. The combination of multiple drivers increases the human pressures on

species and their habitats and makes effective conservation strategies for biodiversity very much needed.

However, some fractions of biodiversity have been neglected in conservation. Desiccation-tolerant vascular plants (DT plants) are a good example of this. Also referred to as “resurrection plants” or “poikilohydrous”, DT plants have the remarkable ability to survive water loss up to 95% relative water content (equivalent to 0.1 g H<sub>2</sub>O/g dry weight) and resume their metabolism after rehydration with little or no biomass loss [9,10]. The desiccation tolerance ability is expected to provide an ecological advantage to thrive in environments with repetitive drought events throughout the year [9]. Due to this response, they can offer valuable genetic insights for breeding drought-resistant crops [11,12]. Also because of this response they are often seen as resistant species to environmental changes, and consequently neglected in conservation. However, this assumption is not justified by the current literature. Firstly, DT plants have been reported by earlier studies as sensitive to changes in the environmental conditions (e.g., changes in the length and intensity of drought might exceed the species’ capacity to tolerate desiccation) [9,13]. It means that anthropogenic drivers such as climate change can lead DT plants to not be able to tolerate desiccation in new climatic settings. Moreover, DT plants are associated with inselbergs, which are rock outcrops that abruptly rise from the landscape and act as island-like ecosystems to the species that inhabit them [9,10]. These ecosystems are often overlooked in conservation initiatives and are particularly exposed to land use change (e.g., quarrying) [14], and their insular characteristics [15] can reduce species’ capacity to migrate to new suitable areas in case of habitat loss. Due to these aspects, we believe that DT plants are a good model system to discuss the species neglected in conservation and the potential consequences of overlooking such conservation gaps.

In this study, we raise two research questions. (1) What is the state of knowledge in the conservation of DT plants? (2) Are the current protected areas addressing the conservation needs of DT plants? For this, we focus on West Africa and divide this study in two sections. In the first section, we conducted a systematic review to provide the first comprehensive list of DT plants for West Africa (including information about their distribution and conservation status) and to identify the discussions about DT plant conservation in the region. In the second section, we conducted a study case, in which we assess the protection and exposure of DT plants to two anthropogenic drivers of biodiversity loss: land use change and climate change. In this section, we compiled a list of DT plants reported in a database on West African inselbergs compiled by S. Porembski and compared their exposure to land use and climate change across unprotected and protected areas. We used quarrying activities and departures from the current climate conditions as proxies for land use and climate change, respectively. Despite being focused on DT plants from West Africa, we believe our study provides a basis for constructive discussion about the conservation of species often neglected in conservation and contributes valuable insights for generating more critical thinking about these species’ conservation.

## 2. Results

### 2.1. Diversity, Distribution, and Conservation of DT Plants in West Africa

All together, we found 49 desiccation-tolerant plant species in West Africa from 30 genera and 11 families across lycophytes, ferns, and angiosperms (Table 1). *Asplenium* stood out as the most species-rich genus, with six species reported, followed by *Hymenophyllum* and *Sporobolus* with four and three species, respectively. Poaceae emerged as the most species-rich, with ten species, followed by Pteridaceae and Hymenophyllaceae, respectively, with nine and eight species. Ferns represented 61.22%, angiosperms 36.73%, and lycophytes 2.04% of the species listed.

**Table 1.** Checklist of desiccation-tolerant vascular plants present in West Africa, their distribution in West Africa, and conservation status according to IUCN Red List. BEN—Benin; BFA—Burkina Faso; CIV—Côte d'Ivoire; CMR—Cameroon; CPV—Cabo Verde; GGN—Gulf of Guinea Is.; GHA—Ghana; GIN—Guinea; GMB—the Gambia; GNB—Guinea-Bissau; GNQ—Equatorial Guinea; LBR—Liberia; MLI—Mali; MRT—Mauritania; NER—Niger; NGA—Nigeria; SEN—Senegal; SLE—Sierra Leone; TCD—Chad; TGO—Togo.

|                                                                           | Distribution in West Africa                                     | IUCN Red List Categories |
|---------------------------------------------------------------------------|-----------------------------------------------------------------|--------------------------|
| Lycophytes                                                                |                                                                 |                          |
| Selaginellaceae                                                           |                                                                 |                          |
| <i>Selaginella njamnjamensis</i> Hieron.                                  | BEN, CMR, MLI, NGA                                              | Not evaluated            |
| Pteridophytes                                                             |                                                                 |                          |
| Aspleniaceae                                                              |                                                                 |                          |
| <i>Asplenium aethiopicum</i> (Burm.f.) Becherer                           | CIV, CMR, GGN, GIN, GNQ, LBR, NER, NGA, SLE, TCD                | Vulnerable               |
| <i>Asplenium friesiorum</i> C.Ch.                                         | CMR, GGN, NGA                                                   | Not evaluated            |
| <i>Asplenium megalura</i> Hieron.                                         | CIV, CMR, GHA, GGN, GIN, LBR, SLE, TGO                          | Not evaluated            |
| <i>Asplenium monanthes</i> L.                                             | CMR, GGN                                                        | Least Concern            |
| <i>Asplenium sandersonii</i> Hook.                                        | CMR, GGN, GNQ, NGA                                              | Not evaluated            |
| <i>Asplenium stuhlmannii</i> Hieron.                                      | CIV, CMR, GIN, NGA, SLE                                         | Not evaluated            |
| Dryopteridaceae                                                           |                                                                 |                          |
| <i>Elaphoglossum acrostichoides</i> (Hook. & Grev.) Schelpe               | CIV, CMR, GGN, GHA, GIN, LBR                                    | Least Concern            |
| Hymenophyllaceae                                                          |                                                                 |                          |
| <i>Crepidomanes chevalieri</i> (Christ) Ebihara & Dubuisson               | CIV, CMR, GGN, GHA, GIN, LBR, NGA, SLE                          | Not evaluated            |
| <i>Crepidomanes melanotrichum</i> (Schltdl.) J.P.Roux                     | CIV, CMR, GGN, GHA, GIN, LBR, NGA, SLE                          | Not evaluated            |
| <i>Didymoglossum erosum</i> (Willd.) Beentje                              | CIV, CMR, GHA, GIN, LBR, NGA, SLE                               | Not evaluated            |
| <i>Hymenophyllum capillare</i> Desv.                                      | CMR, GGN, GHA                                                   | Not evaluated            |
| <i>Hymenophyllum hirsutum</i> (L.) Sw.                                    | CMR, GGN, GHA, GIN, GNQ, CIV, LBR                               | Not evaluated            |
| <i>Hymenophyllum kuhni</i> C.Ch.                                          | CMR, GGN, GHA, GIN, GNQ, LBR, NGA, SLE                          | Not evaluated            |
| <i>Hymenophyllum splendidum</i> Bosch                                     | CMR, GNQ                                                        | Not evaluated            |
| <i>Polyphlebium borbonicum</i> (Bosch) Ebihara & Dubuisson                | CIV, CMR, GGN, GNQ, GHA, GIN, LBR                               | Not evaluated            |
| Polypodiaceae                                                             |                                                                 |                          |
| <i>Loxogramme abyssinica</i> (Baker) M.G.Price                            | CIV, CMR, GGN, GHA, GIN, GNQ, LBR, NGA, SLE, TGO                | Not evaluated            |
| <i>Melpomene flabelliformis</i> (Poir.) A.R.Sm. & R.C.Moran               | CMR, GGN                                                        | Not evaluated            |
| <i>Phymatosorus scolopendria</i> (Burm.f.) Pic.Serm.                      | BEN, CIV, CMR, GGN, GNQ, GHA, GIN, LBR, NGA, SLE, TGO           | Not evaluated            |
| <i>Platyterium stemaria</i> (P.Beauv.) Desv.                              | BEN, CIV, CMR, GGN, GNQ, GHA, GIN, LBR, NGA, SEN, SLE           | Not evaluated            |
| <i>Pleopeltis macrocarpa</i> (Willd.) Kaulf.                              | CIV, CMR, GGN, GIN, LBR, NGA, SLE                               | Not evaluated            |
| Pteridaceae                                                               |                                                                 |                          |
| <i>Actiniopteris radiata</i> (Sw.) Link                                   | CMR, CPV, MLI, NGA, TCD, TGO                                    | Not evaluated            |
| <i>Actiniopteris semiflabellata</i> Pic.Serm.                             | MRT                                                             | Not evaluated            |
| <i>Adiantum incisum</i> Forssk.                                           | CIV, CMR, CPV, GHA, NGA, TGO                                    | Not evaluated            |
| <i>Cheilanthes coriacea</i> Decne.                                        | NER, TCD                                                        | Not evaluated            |
| <i>Cheilanthes inaequalis</i> Mett.                                       | CMR, GIN, NGA                                                   | Not evaluated            |
| <i>Cosentinia vellea</i> (Aiton) Tod.                                     | CPV                                                             | Least Concern            |
| <i>Hemionitis farinosa</i> (Forssk.) Christenh.                           | CMR, GGN, NGA, SLE                                              | Not evaluated            |
| <i>Pellaea doniana</i> Hook.                                              | GNQ                                                             | Not evaluated            |
| <i>Vittaria guineensis</i> Desv.                                          | CIV, CMR, GGN, GHA, GIN, GNQ, LBR, NGA, SLE, TGO                | Not evaluated            |
| Tectariaceae                                                              |                                                                 |                          |
| <i>Arthropteris orientalis</i> (J.F.Gmel.) Posth.                         | CIV, CMR, GGN, GHA, GIN, LBR, NGA, SLE                          | Not evaluated            |
| Angiosperms                                                               |                                                                 |                          |
| Cyperaceae                                                                |                                                                 |                          |
| <i>Afrotrilepis jaegeri</i> J.Raynal                                      | SLE *                                                           | Not evaluated            |
| <i>Afrotrilepis pilosa</i> (Boeckeler) J.Raynal                           | BEN, BFA, CIV, CMR, GHA, GIN, GNQ, LBR, MLI, NGA, SEN, SLE, TGO | Not evaluated            |
| <i>Coleochloa abyssinica</i> (Hochst. ex A.Rich.) Gilly                   | CMR, NGA                                                        | Not evaluated            |
| <i>Coleochloa domensis</i> Muasya & D.A.Simpson                           | CMR *                                                           | Critically endangered    |
| <i>Microdracoides squamosa</i> Hua                                        | CMR, GIN, NGA, SLE *                                            | Not evaluated            |
| Linderniaceae                                                             |                                                                 |                          |
| <i>Craterostigma plantagineum</i> Hochst.                                 | BFA, NER, TCD                                                   | Not evaluated            |
| <i>Craterostigma yaundense</i> (S.Moore) Eb.Fisch., Schäferh. & Kai Müll. | CMR *                                                           | Vulnerable               |

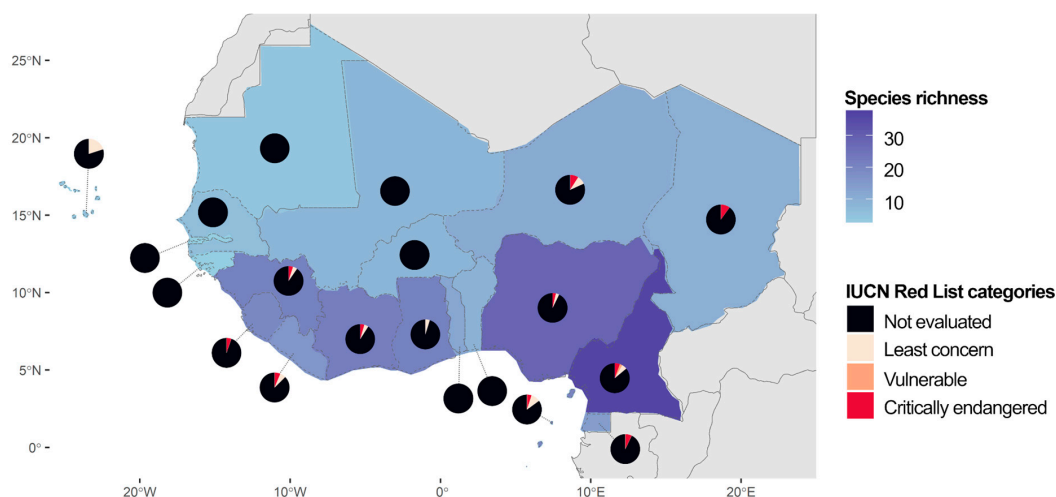
Table 1. Cont.

|                                                              | Distribution in West Africa                                               | IUCN Red List Categories |
|--------------------------------------------------------------|---------------------------------------------------------------------------|--------------------------|
| Poaceae                                                      |                                                                           |                          |
| <i>Microchloa indica</i> (L.f.) P.Beauv.                     | BEN, BFA, CIV, CMR, GHA, GIN, GNB, MLI, NER, NGA, SEN, SLE, TCD, TGO      | Not evaluated            |
| <i>Microchloa kunthii</i> Desv.                              | BEN, BFA, CIV, CMR, GHA, NGA, TGO                                         | Not evaluated            |
| <i>Oropetium aristatum</i> (Stapf) Pilg.                     | BEN, BFA, CIV, GHA, GMB, GNB, MLI, NER, SEN, TGO *                        | Not evaluated            |
| <i>Oropetium capense</i> Stapf                               | MLI, MRT, NER, TCD                                                        | Not evaluated            |
| <i>Sporobolus festinus</i> Hochst. ex A.Rich.                | BEN, BFA, CIV, CMR, GHA, GIN, GMB, GNQ, MLI, MRT, NER, NGA, SEN, TCD, TGO | Not evaluated            |
| <i>Sporobolus pellucidus</i> Hochst.                         | BFA, NER, TCD                                                             | Not evaluated            |
| <i>Sporobolus stapfianus</i> Gand.                           | NER, NGA                                                                  | Least Concern            |
| <i>Tripogon major</i> Hook.f.                                | SLE                                                                       | Not evaluated            |
| <i>Tripogon multiflorus</i> Miré & H.Gillet                  | CPV, NER, TCD                                                             | Not evaluated            |
| <i>Tripogonella minima</i> (A.Rich.) P.M.Peterson & Romasch. | BEN, BFA, CIV, CMR, CPV, GHA, MLI, MRT, NER, NGA, SEN, TCD, TGO           | Not evaluated            |
| Velloziaceae                                                 |                                                                           |                          |
| <i>Xerophyta schnitzleinia</i> (Hochst.) Baker               | NGA, GNQ                                                                  | Not evaluated            |

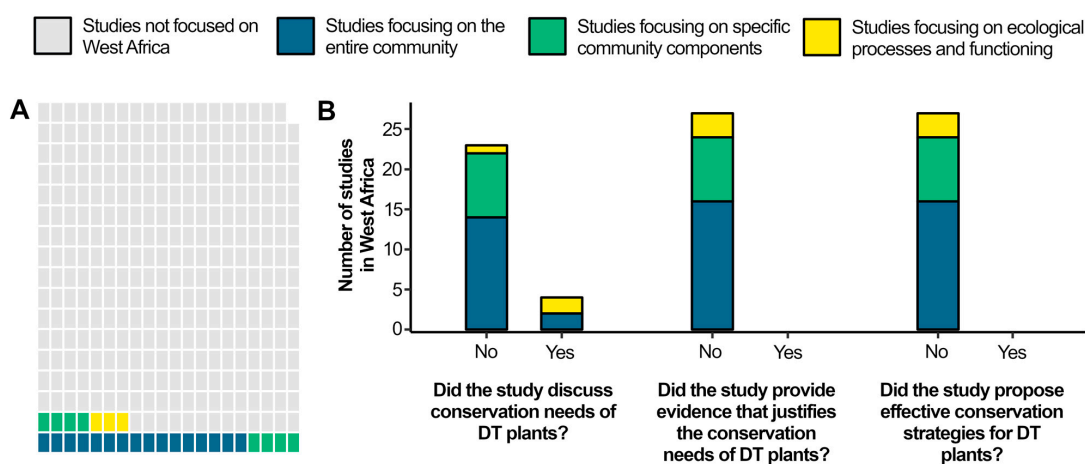
\* endemic to West Africa.

Regarding the distribution of species in West Africa, Cameroon stood out as the country most rich in species (36), followed by Nigeria (28) and Côte d'Ivoire (22; Figure 1). The Gambia and Guinea-Bissau were the countries with the lowest number of species, having two species each. While some species were widespread in West Africa, others were restricted to one or a few countries. *Sporobolus festinus* (Poaceae) was the species most widespread in West Africa, being recorded in 15 countries. On the other hand, seven species were found in only one country in West Africa, including three nationally endemic species: *Afrotrilepis jaegeri* (Cyperaceae), endemic to Sierra Leone, and *Coleochloa domensis* (Cyperaceae) and *Craterostigma yaundense* (Linderniaceae), both endemic to Cameroon. In total, six species are endemic to West Africa. Besides *Afrotrilepis pilosa*, *A. jaegeri*, *C. domensis*, and *C. yaundense*, *Microdracoides squamosa* (Cyperaceae) and *Oropetium aristatum* (Poaceae) also have their distribution restricted to West Africa. Concerning the conservation status of the DT plants in West Africa, for the majority of the DT plants from West Africa, 42 species (86%) have not been evaluated for conservation by the IUCN. Only seven species (14%) have been evaluated, among which four species were classified as Least Concern (*Asplenium monanthes*, *Elaphoglossum acrostichoides*, *Cosentinia vellea*, and *Sporobolus stapfianus*; Aspleniaceae, Dryopteridaceae, Pteridaceae, and Poaceae, respectively), two species as vulnerable (*Asplenium aethiopicum* and *C. yaundense*; Aspleniaceae and Linderniaceae, respectively), and one species as critically endangered (*C. domensis*; Cyperaceae). A complete lack of assessment of DT plants for conservation was registered in eight countries in West Africa (40%). While 12 countries (60%) have at least one species assessed by IUCN, most species in those countries have not yet been assessed concerning their conservation.

Out of the 339 studies, only 27 studies (7.9%) were focused on West Africa (Figure 2; Table S4). Most of these 27 studies were focused on the entire community in which DT plants are embedded (16 studies, 4.7%). Eight studies focused on specific community components (2.3%), while only three studies focused on ecological processes and functioning (0.8%). Among those studies, only four (1.2% of studies, or 15% of studies on DT plants of West Africa) mentioned the conservation needs of DT plants [14–17], although no studies either produced enough evidence to justify the conservation needs of DT plants or proposed effective conservation strategies for DT plants. Of these four studies that mentioned the conservation needs about DT plants, two focused on the entire community [15,17], and two focused on the ecological processes and functioning [14,16] of the DT plants that have been found in an ecological context.



**Figure 1.** Number of desiccation-tolerant vascular plant species in West Africa per country (species richness) and their conservation status according to IUCN Red List categories.



**Figure 2.** Number of studies on desiccation-tolerant vascular plants selected in our systematic review by 3 established categories. (A)—number of studies with explicit focus on West Africa; (B)—number of studies addressing conservation aspects of desiccation-tolerant plants in West Africa according to 3 questions raised.

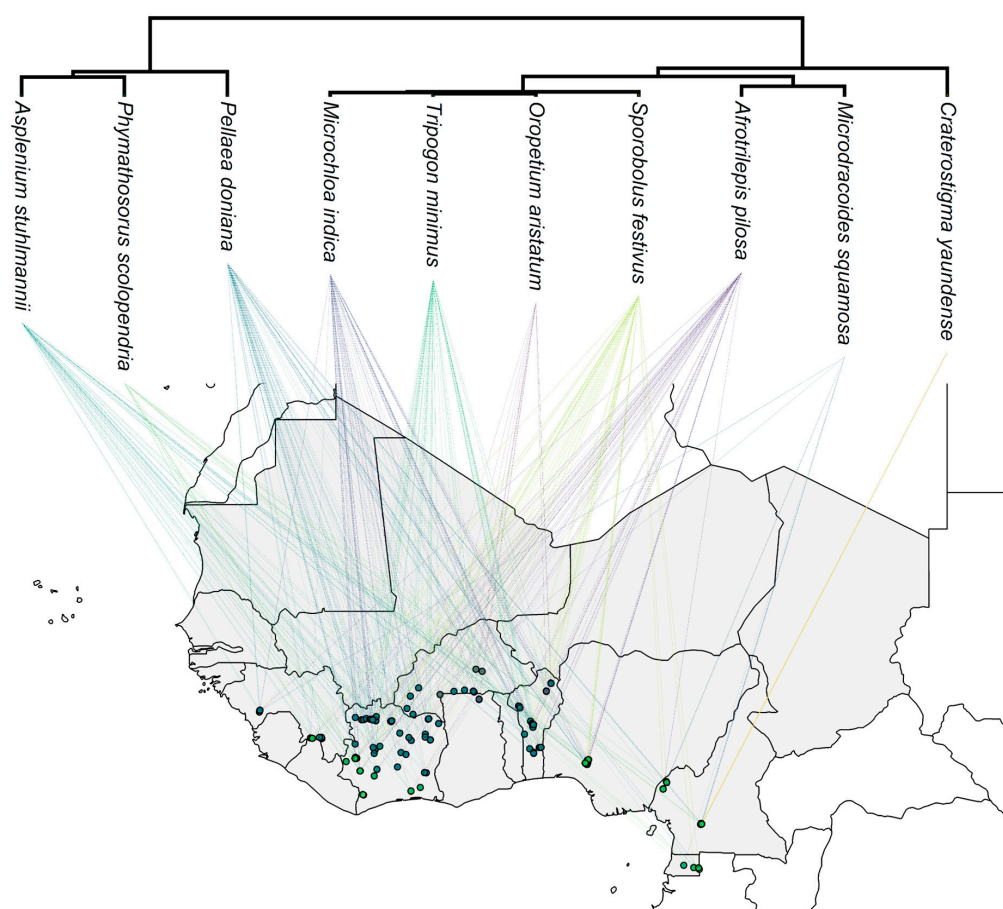
## 2.2. The Exposure of DT Plants to Anthropogenic Drivers of Biodiversity Loss and Their Protection on West African Inselbergs

We compiled a list of 123 inselbergs (spanning from Guinea to Equatorial Guinea) and selected 10 DT plants with an uneven and overlapping distribution across West African inselbergs: *Asplenium stuhlmannii* (Aspleniaceae); *Phymathosorus scolopendria* (Polypodiaceae); *Pellaea doniana* (Pteridaceae); *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae); *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minimus*, and *Sporobolus festivus* (Poaceae); and *Craterostigma yaundense* (Linderniaceae; Figure 3, Table S5). These species form a diverse set of DT plants from taxonomic and geographical perspectives. For instance, while *A. stuhlmannii*, *P. doniana*, *S. festivus*, and *A. pilosa* have a broad-ranging distribution, *P. scolopendria*, *O. aristatum*, *M. squamosa*, and *C. yaundense* were registered on fewer inselbergs.

While a significant difference between the unprotected and protected areas was registered in relation to the species' exposure to quarrying, the species' exposure to climate change was similar across the protected and unprotected inselbergs in all future scenarios (Table 2; a Mann–Whitney U test was conducted for species exposure to quarrying and *t*-test for species exposure to climate change). However, we could observe marked patterns among species protection and exposure to quarrying and climate change. Firstly, it is



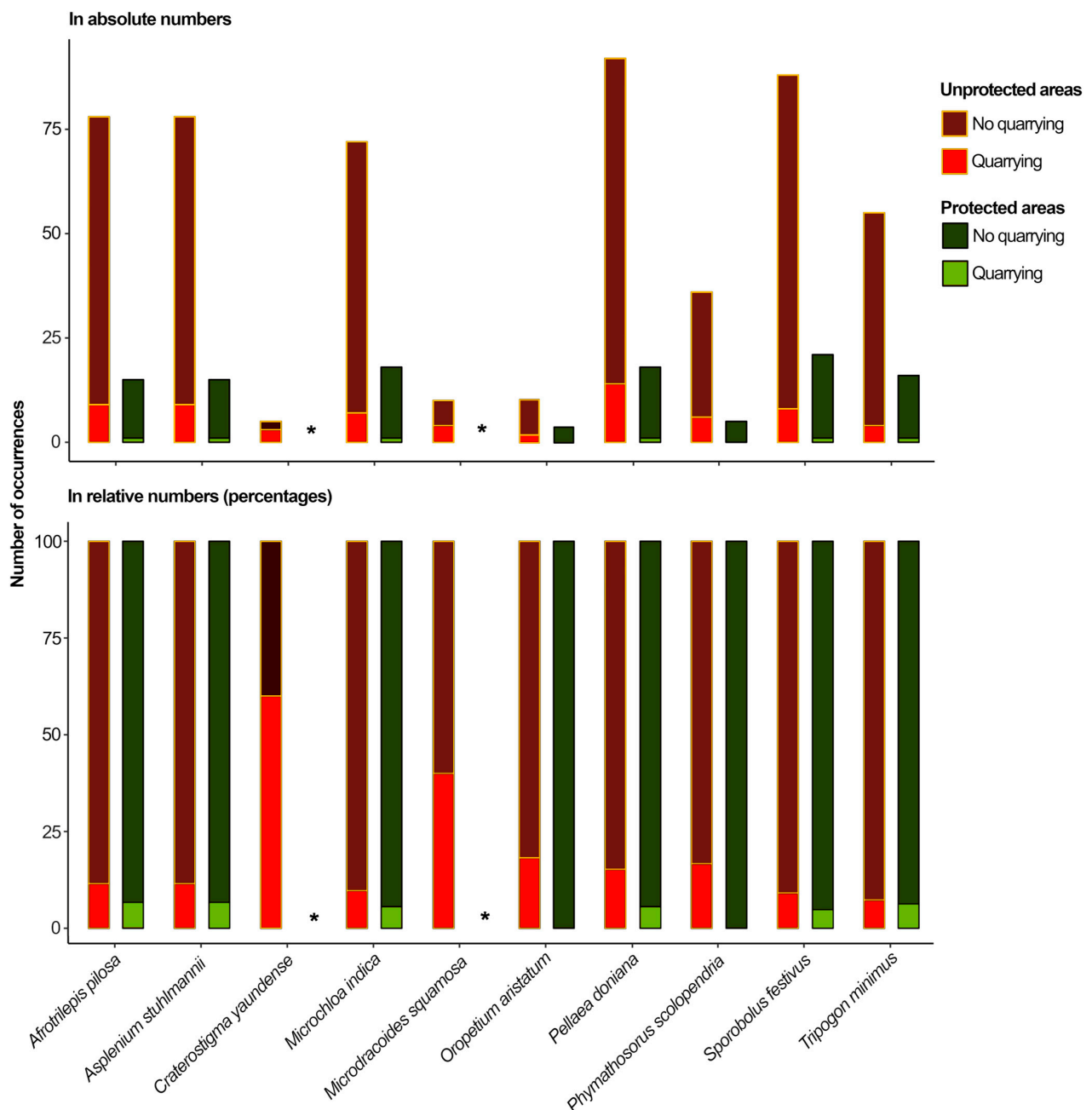
important to highlight that *C. yaundense* and *M. squamosa* were not present within the protected areas. Regarding the species' exposure to quarrying, we found that all the species had at least one plant on an inselberg in which quarrying was registered (Figure 4; Table S6). While *T. minimus* had the lowest relative level of exposure to quarrying (7% of inselbergs, i.e., five out of seventy-one), *C. yaundense* showed the highest relative level of exposure to quarrying (60% of inselbergs, i.e., three out of five). The exposure of all the species to quarrying was reduced in absolute and relative values when inselbergs were included in the protected areas. While *T. minimus* had the lowest relative reduction in exposure to quarrying in protected areas (1.1 times less exposed to quarrying), *O. aristatum* and *P. scolopendria* had their exposure to quarrying reduced from 18% and 17%, respectively, to 0% (Table S7).



**Figure 3.** Uneven geographical distribution of 10 desiccation-tolerant vascular species across 123 inselbergs in West Africa.

**Table 2.** Comparison between unprotected and protected areas in relation to species exposure to quarrying and climate change. We conducted Mann–Whitney U test to analyze species' exposure to quarrying and *t*-test to analyze species' exposure to climate change. *p*-values for species exposure to climate change were adjusted by Bonferroni correction.

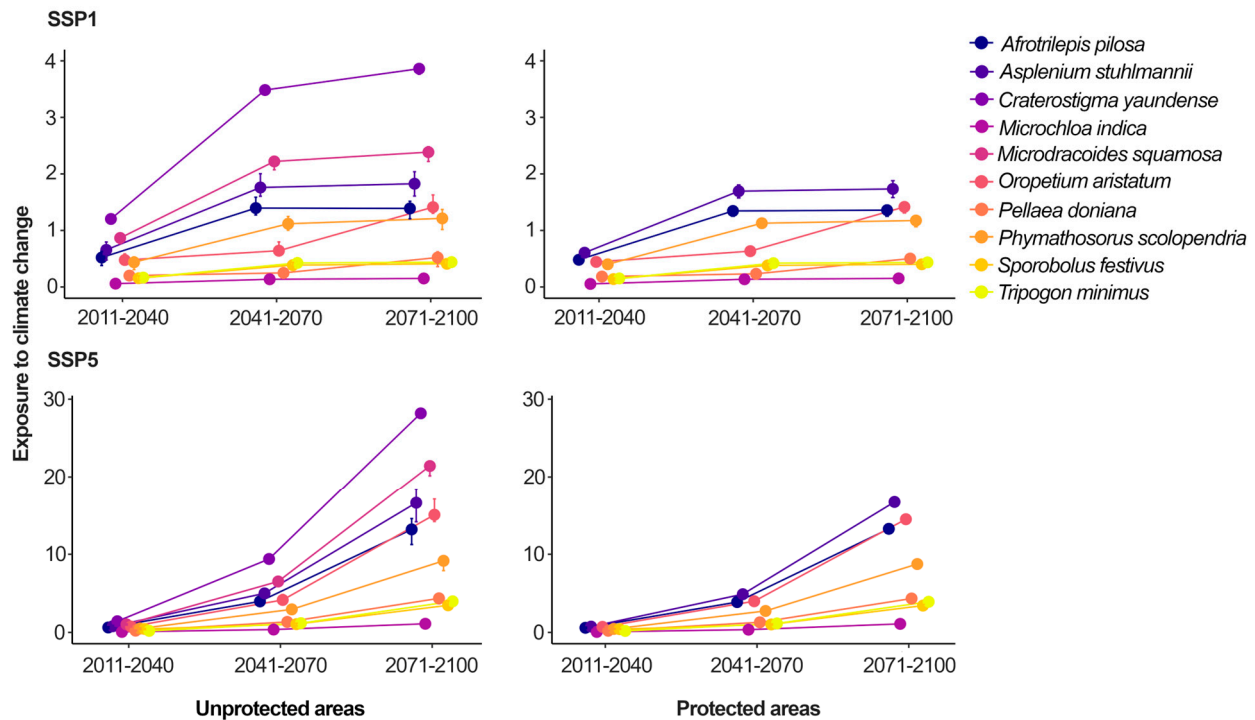
|                | W-Value/t-Value | <i>p</i> -Value |
|----------------|-----------------|-----------------|
| Quarrying      | 80              | 0.0004          |
| Climate change |                 |                 |
| SSP1           |                 |                 |
| 2011–2040      | 1.17            | 0.7809          |
| 2041–2070      | 1.04            | 0.9456          |
| 2071–2100      | 1.05            | 0.9297          |
| SSP5           |                 |                 |
| 2011–2040      | 1.1             | 0.8592          |
| 2041–2070      | 1.03            | 0.9519          |
| 2071–2100      | 0.93            | 1               |



**Figure 4.** The impact of quarrying on the habitats of the 10 evaluated plant species. This figure illustrates the extent of exposure to quarrying for each species in unprotected and protected areas in both absolute and relative numbers. \*—no presence of the species was registered in such areas.

Concerning the species' exposure to climate change, all the species were more exposed to climate change in the most pessimistic scenario (SSP5) when compared to the most optimistic scenario (SSP1), especially in the farthest future (i.e., time-series 2071–2100; Figure 5, Table S8). *M. indica* was the species with least exposure to climate change, although its exposure scores increased 2.5-fold over time in the most optimistic scenario (i.e., increasing from 0.06 to 0.15 in the 2011–2040 and 2070–2100 time-series, respectively) and 18.3-fold in the most pessimistic scenario (i.e., increasing from 0.06 to 1.1 in the 2011–2040 and 2070–2100 time-series, respectively). On the other hand, *C. yaundense* was the species most exposed to climate change, reaching an exposure score 25.6 times higher than that of *M. indica* in the most pessimistic scenario of the farthest future. *C. yaundense* also showed greater rises in its exposure to climate change over time, increasing 3.2-fold in

the most optimistic scenario (i.e., increasing from 1.2 to 3.86 in 2011–2040 and 2071–2100, respectively) and 19.7-fold in the most pessimistic scenario (i.e., increasing from 1.48 in 2011–2040 to 28.18 in 2071–2100).



**Figure 5.** Projected climate change exposure of 10 desiccation-tolerant plants in West Africa under Low (SSP1) and High (SSP5) Emission Scenarios (2011–2100). This figure illustrates projected mean exposure of 10 desiccation-tolerant plant species to climate change under two different climate scenarios: SSP1, representing low-emission, sustainable pathway; and SSP5, high-emission, fossil-fuel-intensive pathway. Projections are shown across time-series: 2011–2040, 2041–2070, and 2071–2100.

### 3. Discussion

Our literature review reveals that DT plants form a diverse group in West Africa, but are a largely neglected group of species in conservation as are their habitats. Only seven species (14%) have been evaluated for conservation by the IUCN, and conservation issues with DT plants were only mentioned by four studies, although in an indirect way and without producing enough evidence to justify their need for conservation. We argue that conservation-explicit assessments are ultimately necessary to ensure the conservation of DT plants. Moreover, we recommend that instead of relying on general conservation narratives, future studies focus on a mechanistic understanding of species conservation needs in order to support efficient conservation strategies for DT plants.

Our case study revealed an important bias of protected areas towards certain species, besides its differential capacity to minimize the impact of the different anthropogenic drivers of biodiversity loss. Among the ten selected DT plants, two species (i.e., *M. squamosa* and *C. yaundense*) were not present within the protected areas. This is especially critical when considering that they are the species with the highest exposure rates to quarrying and climate change and are the two rarest species in our species pool. Conservation efforts must reduce such protection bias by explicitly including overlooked species in their conservation objectives. However, the conservation objectives must take into account the specific anthropogenic threats in each case. We found that the protected areas were more effective in mitigating the direct effects of human activities such as quarrying. However, they showed little effect on species exposure to climate change. We suggest, for example,



using protected areas to ensure the connectivity among inselbergs as a more efficient strategy to cope with climate change.

### 3.1. *The Need of Studies Specifically Designed to Assess the Conservation of DT Plants*

Only four studies mentioned the need for the conservation of DT plants or their habitats. Two of them focused on the entire plant community (i.e., [15,17]), and two others focused on ecological processes and functioning (i.e., [14,16]). Even though they are not explicitly targeting DT plants, these studies either highlighted the ecological singularity of a species in the ecosystem DT plants occur (i.e., inselbergs), or acknowledged threats to its biodiversity in order to claim their need for conservation. However, those studies did not produce enough evidence to justify their claims. We acknowledge that it was not the aim of any of the mentioned studies to measure species conservation needs to support conservation efforts. However, we need studies explicitly designed to assess and discuss the conservation of DT plants. We believe conservation initiatives on DT plants would benefit from going beyond general conservation narratives towards a mechanistic understanding of species conservation needs.

The vulnerability framework suggested by Dawson et al. [18] is a good starting point to understand the mechanisms that lead DT plants to need conservation action, if they do. Dawson et al. [18] describe species vulnerability to environmental changes as a result of their exposure (i.e., the magnitude of changes a species undergoes), sensitivity (i.e., how much a species is affected by changes) and adaptive capacity (i.e., how much a species can mitigate the negative effects of environmental changes). According to this framework, species conservation needs increase under high-level exposure, high sensitivity, and low adaptive capacity. By identifying the importance of each component in the species vulnerability equation (i.e., exposure, sensitivity, and adaptive capacity), conservation initiatives can be more effective by strategically intervening in the critical component for the species in question. For example, we could assume that different DT plants in a same community are similarly exposed to a given threat. But the species' sensitivity and adaptive capacity to this threat is likely to vary across species. Especially, we must consider that DT plants are found in 11 plant families in West Africa and desiccation tolerance has independently re-evolved across vascular plants' phylogeny [19] (please also see Dollo's Law [20]). If attempts to reduce species' exposure to threats fail (e.g., local decision-makers cannot stop climate change effects in a given location), conservation strategies for species with high sensitivity, but high dispersal capacities (i.e., high adaptive capacity) might focus on ensuring species migration to new suitable locations (e.g., increasing the connectivity between protected areas and monitoring species movement and biotic interactions). However, if the species have high sensitivity and a low dispersal capacity (i.e., low adaptive capacity), more intensive conservation interventions might be taken to ensure the species will not go extinct in the wild (e.g., decision-makers could opt for assisted migration in order to guarantee that one species will not go extinct in the wild).

Understanding those three components is not always an easy task. Scientists and conservationists might encounter challenges in assessing some components (e.g., species can mitigate the negative effect of changes in many ways, from showing high genetic diversity to dispersing to new suitable areas) [18] and available resources are insufficient to evaluate every species at the proper time [21]. Studies with a focus on communities or their components could attempt to identify species to be prioritized for a posterior mechanistic conservation assessment. For DT plants, we have incomplete information about which species require more attention for conservation. We found that 86% of the species recorded have not yet been assessed for conservation under the IUCN Red List framework, as eight countries have not evaluated DT species; aligning with the general underrepresentation of

West African plant species in global conservation assessments [22]. Although providing systematic and conservation-explicit guidelines for species conservation, the IUCN Red List framework might also be costly and time-consuming. For instance, monitoring population size reduction (Criteria A from the IUCN Red List framework) recommends measures over 10 years or three generations [23]. Alternatively, quicker (yet robust) assessments could also be used to inform about priority species for conservation (e.g., [24–26]) and which species the vulnerability framework from Dawson et al. [18] can be applied to for more effective conservation initiatives.

The studies we analyzed had a different approach. For example, some studies highlighted threats to inselberg species, including DT plants, to justify species conservation needs. Porembski [16] discussed that stress-tolerant native inselberg species can be out-competed by invasive species with a better competitive ability. Invasive species will only establish themselves in a new community if they either have plant responses that confer greater fitness under local environmental constraints (i.e., “trying harder” strategy) or similar fitness when compared to that of local species (i.e., “joining the locals” strategy [27], but see also [28]). That means that in ecosystems in which environmental stress is supposed to be the strongest ecological constraint such as inselbergs, invasive species must either be fit enough to overcome environmental stress compared to local species or at least similarly fit in order to avoid being excluded by local species. Otherwise, we would be simply overestimating the impact of an alien species with neutral (or even positive) effects on the existing community [29,30]. We argue that invasive species with a better competitive ability would only be a threat in inselbergs if human pressures led to a shift in the importance of different ecological constraints. For example, over-visitation by humans or the introduction of grazing animals in inselbergs might intensify disturbance events (i.e., any external constraint that cause partial or total biomass loss; sensu Grime [31]) and reduce the relative importance of environmental stress (i.e., any external constraint that reduce plants productivity; sensu Grime [31]) in shaping inselberg plant communities. This shift would lead ruderal invasive species to exclude native species using the “trying harder” strategy because they are fitter under such new conditions (e.g., [32]). Thus, we support new studies focused on ecological processes that either monitor trends in species populations or habitat shifts over time with the presence of a potentially invasive species (e.g., [33]) or assess the changes in functional traits among native species due to the presence of newcomers (e.g., [34]). For DT plants, we believe that such studies could advance discussions about the invasiveness of inselbergs and their impact on DT plants.

Another common reasoning to justify the conservation needs of inselberg species, including DT plants, is that many plants exhibit particular responses to environmental challenges (e.g., “specializations” or “adaptations”) and that they have a restricted distribution (e.g., sometimes endemic to inselbergs). These two factors might reinforce the need for monitoring such species or ecosystems. However, there is not enough justification to prioritize a species for conservation. Concerning the particular responses to environmental challenges, we must keep in mind that such responses might also be beneficial to cope with some anthropogenic drivers of biodiversity loss. Desiccation tolerance allows for plants to overcome droughts with little or no biomass loss. If drought events become more frequent, intensive, and extensive owing to climate change, and thus lead plants to experience high dehydration or desiccation rates, one might logically argue that DT plants are not as sensitive to climate change as desiccation-sensitive plants. Regarding species-restricted distribution, the expectancy of higher extinctions risks for these species is often related to their narrow niche breadths unfolding a lower tolerance to changes and small population sizes, pushing species close to the viable population thresholds (i.e., minimum number of individuals required for the species to not go locally ex-

tinct) [35,36]. However, niche is not the only constraint to species distribution patterns (dispersal is also an important cause of the species restricted distribution). This means that species with restricted distribution are not necessarily sensitive to changes. Moreover, the species might be rare on a regional scale, but dominant on a local scale [37], so they are not close to the viable population thresholds. For instance, despite *A. pilosa* being endemic to West Africa and restricted to inselbergs, it can be present in very distinct environmental settings (e.g., locations where annual precipitation varies from less than 1000 to more than 3000 mm [38]) and achieve high abundances within local communities [39]. A species might indeed require conservation attention, but not necessarily because they have particular responses to the environment or because they have restricted distribution. We need more lines of evidence to evaluate species' conservation needs rather than simply rely on clues that, despite their usefulness, may not appropriately describe species' vulnerability to the anthropogenic drivers of biodiversity loss.

However, particular responses to environmental challenges (i.e., desiccation tolerance in our context) and restricted distribution are appealing features of DT plants and can be possibly used to encourage conservation awareness about DT plants. For example, the three Red Listed species *A. aethiopicum*, *C. domensis*, and *C. yaundense* could play an important role as Cinderella species in the context of DT plants in West Africa. *C. yaundense* is an inselberg-endemic species found only within the urban area of Yaoundé (the capital of Cameroon). Cinderella species are a type of surrogate species (i.e., species that are strategically used by conservation initiatives to promote the conservation of other species [40]) that are endangered, and despite not being as famous as flagship species, have enough charisma or public appeal to improve support on conservation initiatives [40–42]. These three species could be used in coordination to better capture the phylogenetic and ecological diversity specific to each area (e.g., as flagship fleets; see [43,44]). However, raising public awareness of plant species is trickier than for animals, but not an impossible task [45]. Alternative solutions should not be neglected, such as using umbrella species (i.e., another type of surrogate species, but which are more common features in the landscape, thus more likely to have stronger connections with local communities [46,47]), or other plant or animal species that occur on rock outcrops and would help conserving DT plants (since many DT plants are associated with these ecosystems). Moreover, we must keep in mind that the use of surrogate species in conservation initiatives risks us failing to solve complex problems through simplistic solutions [48]. Future studies are still necessary to select appropriate surrogate species and evaluate if such strategies satisfy local ecological realities.

### 3.2. Protected Areas Are Not Similarly Effective in Face of Different Conservation Challenges

The species with more exposure to anthropogenic threats to biodiversity (i.e., *C. yaundense* and *M. squamosa*; Figure 6) are the ones not included in the existing protected area networks. This pattern is especially worrying if we consider that they are the two rarest species in our study, as this feature is linked with greater extinction risks [49,50]. Moreover, while *C. yaundense* is classified as vulnerable by the IUCN, *M. squamosa* is currently unevaluated by the IUCN, hindering our understanding about the conservation needs of one of the species that might most require our attention. Aichi Target 11 of the Convention on Biological Diversity [50] aimed to protect at least 17% of terrestrial areas by 2020 in an equitable and ecologically representative way (and 30% by 2030 according to Target 3 of the Kunming-Montreal Global Biodiversity Framework) [51]. However, despite the 17% threshold reached in 2024 [52], our results show that ecological representativeness has not been yet met. It is estimated that nearly 60% of vascular plant diversity hotspots still remain outside protected areas, leaving many endemic and vulnerable species unprotected despite international conservation targets [53]. We believe that reducing the protection bias



towards certain ecosystems and species requires the adjustment of conservation objectives to explicitly include overlooked species, such as *C. yaundense* and *M. squamosa*.



**Figure 6.** Species that most require conservation attention and suffer anthropogenic threats to their diversity are ones least favored by current protection areas. (A)—*Microdracoides squamosa* (Cyperaceae); (B)—*Craterostigma yaundense* (Linderniaceae); (C)—quarrying activities causing removal of desiccation-tolerant vascular plants; (D)—possible effects of climate change on desiccation tolerance ability of desiccation-desiccation vascular plants. Red arrows point to branches of *M. squamosa* that did not tolerate desiccation and rehydration cycles.

However, simply assigning protection areas might not be sufficient to ensure species protection against the anthropogenic drivers of biodiversity loss. In our study, the protected areas may have provided effective buffering against the direct effects of human activities such as quarrying (Table S7). However, they were less effective in mitigating the indirect effects of human activities such as climate change (Table S8). For instance, species like *O. aristatum* and *P. scolopendria* had their exposure to quarrying reduced to zero in the protected areas, but had roughly the same level of exposure to climate change when comparing the protected and unprotected inselbergs (in some futures scenarios, their level of exposure to climate change was higher in protected areas). Thus, the reasoning for using protected areas to reduce quarrying rates is more straightforward. By establishing protected areas, we can avoid quarrying activities in quarrying-prone areas, which are often neglected by conservation initiatives [14], and in which, species often have small geographic ranges [54]. Mitigating the impacts of quarrying may demand stricter land-use regulation and site-level protection. For example, some species were found on inselbergs included in a protected area, but with evidence of quarrying. Expanding the protection areas that include inselbergs and satisfy the conservation objectives (e.g., 30% under protection by 2030) requires enough resources to ensure the protection of established

protected areas. We do not think it is the responsibility of researchers to find solutions for resource mobilization. But future studies on the conservation of DT plants could provide more evidence on the effectiveness of different conservation approaches to support resource mobilization campaigns, as recommended by the Analysis of the Strategic Plan 2011–2020 of the Convention on Biological Biodiversity [55].

Alternatively, protected areas should be planned more strategically when considering climate change. For example, we should not expect to stop climate change by demarking a protected area, although using protected areas to establish dispersal corridors for species' possible migration is a more realistic strategy. There is a non-linear negative relationship between habitat loss and the persistence of species, which requires a habitat of minimal size and structure to maintain viable populations [56,57]. That is, a species' probability of persistence gradually decreases with habitat loss until the connectivity among the remaining habitat patches in which a species exists reaches a point of no return for species persistence [57]. Here, habitat connectivity depends on factors, such as patch size and its spatial arrangement, besides how species interact with the landscape [57,58]. We believe that conservation planning that can cope with climate change can provide a better understanding of how habitat loss owing to climate change threatens species persistence. Future studies could evaluate the impact of inselberg size and isolation in species metapopulations as to assess the capacity of species to keep gene flow across different inselbergs. Ensuring connectivity among habitat patches where DT plants exist effectively is certain to combat other anthropogenic threats, but we argue it should be more explicitly established as one of the protection area objectives against climate change.

Our study considered only exposure to anthropogenic threats, offering a partial picture of species vulnerability. The fact that the two most exposed species are the most rare and unprotected ones should raise our awareness, but it is noteworthy to mention that high-level exposure does not necessarily translate into higher extinction risks. For example, although highly exposed to climate change, *O. aristatum*, an annual species, might be able to complete its life cycle before extreme climatic conditions and escape, to some extent, the negative effects of climate change. On the other hand, species might face high extinction risks even under modest exposure due to their narrower ecological tolerances [59]. For instance, most Hymenophyllaceae species occur as epiphytes in moist forests and are often sensitive to changes in the desiccation rate due to the lack mechanisms to reduce water loss (e.g., lack of cuticles) [60]. Alternatively, different anthropogenic threats can act in combination, causing additive effects on each other and intensifying their impact on species [3]. Moreover, we only used two anthropogenic threats as proxies for the different drivers of biodiversity loss. For instance, *M. indica* showed the least exposure to climate change, but its broader occurrence across different ecosystems might expose this species to threats that inselberg-endemic species are not subjected. Lastly, we also advocate for future studies that not only use multiple lines of evidence to assess species vulnerability, but that also encompass a greater array of threats (e.g., direct exploitation and invasive alien species) to improve our understanding of species conservation needs and support efficient conservation initiatives.

## 4. Materials and Methods

### 4.1. Study Area

For the purposes of this study, we considered West Africa as a biogeographic region extending from Senegal to Equatorial Guinea, following a broad ecological definition that includes approximately 20 countries and encompasses humid and transitional vegetation zones, as described by the *Encyclopædia Britannica* [61]. This includes countries such as Cameroon, Chad, and Equatorial Guinea, which are politically classified as part of Central

Africa, but share strong ecological and floristic continuity with the West African forest zone. This area spans a strong climatic gradient, with annual rainfall ranging from 250 mm in the arid north to 3000 mm in the humid forest regions. As a result, there are four major vegetation zones in West Africa: the Guineo-Congolian Zone (regional center of endemism), the Guineo-Congolian/Sudanian Zone (transitional zone), the Sudanian Zone (regional center of endemism), and the Sahel Zone (transitional zone). One of the most important ecosystems in this region is the Guinean Coastal forest, which served as a refuge for many species during historical climate fluctuations in the Pleistocene. Today, it remains one of Africa's eight biodiversity hotspots, characterized by high species endemism. However, only 15% of its original forest cover remains [62], motivating conservation efforts, in which 90% of national protected areas are forests [63]. Inselbergs are usually overlooked, unless embedded in protected areas.

#### 4.2. Desiccation-Tolerant Vascular Plants in West Africa

First, we conducted a systematic literature review in order to obtain a list of DT vascular plants and to evaluate their conservation concerns in West Africa. For this, we applied the key-word combination “desiccation tolerant” OR “resurrection” AND angiosperm\* OR pteridophyte\* OR lycophyte\* OR vascular OR plant\*” for the search engines (1) Scopus, (2) Web of Science, (3) Academia, and (4) Google Scholar from 1950 to 2024. We initially retrieved a total of 1657 documents (243 documents from Scopus, 567 from Web of Science, 36 from Academia, and 811 from Google Scholar). After compiling this literature pool, we started cleaning it by removing 549 duplicated records. Then, we removed 1322 documents that were either not subjected to a peer-reviewed process (e.g., grey literature), or which were not considered in the scope of our study, such as publications that did not focus on plants as their main research objective (e.g., studies on geology or zoology). After this step, an addition of 4 articles were included in our literature pool [16,64–66]. They were considered important articles in the context of our study and were not found by the abovementioned key-word search. In total, 339 publications were retained and used in our analyses.

We compiled a comprehensive list of desiccation-tolerant plant species in West Africa. Additionally, we provided information about their geographical distribution in West Africa and conservation status. Information on the distribution of these species in West Africa was compiled from *The Flora of West Africa* [67], *Flora of savannas and rock outcrops of Côte d'Ivoire* [68], and *Plants of the World Online* [69]. Here, we used their occurrence at the country level to discuss species distribution patterns and estimate the diversity patterns of DT plants in West Africa (calculating species richness by country, i.e., number of different species occurring in the same country). The following countries were considered in our study: Benin, Burkina Faso, Côte d'Ivoire, Cameroon, Cabo Verde, Chad, the Gambia, Ghana, Guinea, Guinea-Bissau, Equatorial Guinea, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone, and Togo. In this study, we followed the classification of *Plants of the World Online* [69] and grouped into the Gulf of Guinea, the islands of Bioko, Príncipe, São Tomé, and Annobón.

About their conservation status, we examined species inclusion in the IUCN Red List of Threatened Species version 2025-1 [70]. We used the IUCN Red List 9 categories. The categories (i) extinct and (ii) extinct in the wild indicate species are either found extinct, or only have individuals living outside their natural habitat. Species threatened with extinction are found in the categories (iii) critically endangered, (iv) endangered, and (v) vulnerable, in which their extinction risk decreases in the order given. Those categorized as (vi) near-threatened and (vii) Least Concern are not considered as being at risk of extinction. At last, a lack of assessment exists for species in the categories (viii) data-



deficient and (ix) not evaluated, which have insufficient information for assessment, or simply have not yet been assessed for conservation.

Then, to evaluate the current state of research and discussion about the conservation of DT plants in West Africa, we calculated the number of studies that focused on West Africa and raised three questions: (i) Did the study discuss the conservation needs of DT plants? (ii) Did the study produce enough evidence to justify the conservation needs of DT plants? (iii) Did the study propose effective conservation strategies for DT plants? For instance, we considered that the study discussed conservation needs for DT plants if it identified DT plants as vulnerable or as strategic components for biological conservation. Using this example, we considered that the study produced enough evidence to justify the conservation needs of DT plants if it quantitatively measured the vulnerability of species or its relevance to any facet of diversity in the ecological contexts they occur (i.e., either taxonomic, phylogenetic, or functional diversity). For the third question, we considered that this study proposed effective conservation strategies for DT plants if it suggested, for example, priority species or locations for conservation. To improve our understanding about patterns among those studies, we grouped them in three categories: (1) studies focusing on the entire community, (2) studies focusing on specific community components, and (3) studies focusing on ecological processes and functioning. While we included in the first group studies that focus on the diversity and ecological patterns of the whole community, in the second group, we included studies in which such patterns are discussed from the perspective of particular habitat types or taxonomic/functional groups. Lastly, we included in the third group of studies whose main objective was to discuss the ecological phenomena that explain how community patterns come about, either focusing on the whole community or specific community components.

#### *4.3. Study Case to Evaluate the Exposure of DT Plants to Land Use Change and Climate Change*

We compiled a list of DT plants reported by S. Porembski in a database on West African inselbergs as a result of extensive fieldwork in the region from 1986 to 2024. Only the inselbergs from this database were included in all our analyses. First, as a rough descriptor of the conservation efforts for each species, we counted the number of inselbergs in which each species exist that are included in protected areas and other effective area-based conservation measures using the World Database on Protected Areas [52]. Here, inselbergs in which species exist were categorized into two groups, protected and unprotected.

We focused on species exposure to two anthropogenic drivers of biodiversity loss: land use change and climate change. First, we use optical evidence of quarrying activities on the inselbergs the selected DT plants exist on to estimate species exposure to land use change. For this, we used Google Earth Engine, a cloud-based geospatial analysis platform [71]. Sentinel-2 imagery (QA60 band) was retrieved, and a 2 km radius buffer was applied around each focal location and the surrounding area based on the geographical coordinates of inselbergs from the database of S. Porembski. Then, we produced a composite image for the months between October and December of the two consecutive years of 2022 and 2023, applying a cloud mask (cloud cover of less than 5%) to ensure data quality. The selection of the same months across consecutive years (2022 and 2023) minimizes seasonal variability, allowing us to better compose the obtained images. The period from October to December was chosen because cloud cover was reduced, which allowed us to use more images with a cloud cover < 5%, improving image clarity and the quality of our composite images.

Then, we used the departures in climatic variables for the inselbergs the selected DT plants exist on to estimate their exposure to climate change. For this, we conducted climate niche factorial analysis [72] to obtain information about shifts in climatic variables within the inselbergs. We first modeled species distribution for each species using the distribution

records of species available in the database Global Biodiversity Information Facility [73] (see Table S1). The species occurrence data were harmonized, eliminating duplicates, errors, and uncertain geographic entries. We used the information provided by the database Plants of the World Online [69] as a reference for the natural occurrence of species. We also retained records that despite a lack of geographic coordinates, included detailed location information. Here, we employed the centroid of the municipality. To model species distribution, we used the modelling technique MaxEnt [74] and the bioclimatic variables available in the CHELSA dataset (Table S2) [75] at a spatial resolution of 2°30'. We excluded bioclimatic variables 6, 9, 10, and 11, representing temperature extremes and seasonal means, due to their high collinearity with the other variables. Removing them reduces redundancy and helps avoid overfitting in climate-based models, ensuring more robust and interpretable results. The MaxEnt technique was chosen because of its high predictability to identify suitable areas of occurrence for species from a niche-based perspective, even for taxa with only a few occurrence data [76]. We used only one observation within a 1 km radius and selected the most important environmental variables for each modelled species with a low level of correlation. These steps were considered in order to mitigate sampling bias effects (assuming that species populations are found within isolated rock outcrops and more than one sampling point can be registered for the same inselberg) and to avoid issues with multicollinearity and model overfitting. As for final distribution, we used the consensus of binary maps (i.e., presence–absence) between at least 50% of 5 ensemble MaxEnt models, in which accuracy was higher than 0.8 and 0.6 according to the receiver operator characteristic curve and true skill statistic tests, respectively. To produce the binary maps, we used the individual model thresholds given by MaxEnt in order to maximize the true positive and true negative rates. The evaluation of model accuracy was performed with cross-validation using the k-means method ( $k = 5$ ), in which we used 100, 1000, or 10,000 random background points if the species had less than 30, less than 300, or at least 300 occurrence points, respectively [77].

We conducted climate niche factorial analysis using the same most important bioclimatic variables that explain each species' distribution. In this analysis, the present conditions were compared to the future conditions. For the future, two Representative Concentration Pathway scenarios were used, with SSP1 being the less-severe (sustainable path with environmental boundaries and low greenhouse gas emission) and SSP5 being the worst (very high greenhouse gas emissions, with fossil-fueled development). Also, three intervals of time-series were considered: 2011–2040, 2041–2070, and 2071–2100. Climate niche factorial analysis was chosen for its ability to calculate departures from the prevailing climatic conditions across grid cells and provide a single exposure value for each species to climate change. This overall value of departure allows for robust comparison between species, especially when different variables were selected in order to take into consideration species individual sensitivities to environmental conditions [72]. Lastly, we extracted the exposure values for the inselbergs each species exists on.

To compare DT plants' exposure to quarrying and climate change across unprotected and protected areas, we performed a *t*-test when our data was normally distributed and homoscedastic, or a Mann–Whitney U test when our data did not satisfy the assumptions of parametric statistics. Since hypotheses tests were repeated to include different climate change scenarios, we adjusted the *p*-values using Bonferroni correction. For graphic representation purposes, we produced a phylogenetic tree using the phylogenetic hypothesis provided by Jin and Qian (as *Scenario 3*) [78]. All analyses were conducted and all graphical representations were created using the software R, version R.4.2.2 (please see Table S3 for the used R packages) [79].



## 5. Conclusions

This study provides the first comprehensive list of DT plants in West Africa and reveals, for the first time, a significant research gap related to the conservation of these species. Only 14% of the species have been evaluated for conservation by the IUCN, and only 15% of studies on DT plants of West Africa have discussed their conservation needs, but without producing enough evidence to justify their need for conservation. This is especially critical when considering that among the species we assessed, the two species with the lowest level of protection are the ones with the most exposure to quarrying and climate change. Our study highlights an important bias of protected areas towards certain species, and their differential capacity to minimize the impact of the different anthropogenic drivers of biodiversity loss. Protection areas might be effective to reduce quarrying activities in inselbergs, but they likely will not avoid the negative effects of climate change on species. We believe that a similar situation might be found for other species neglected in conservation like DT plants, and our suggestions to make conservation initiatives more effective can also apply to other groups of species. For example, we advocate for more conservation-explicit assessments and a mechanistic understanding of species' conservation needs. This can be conducted by quantitatively evaluating the different components of species' vulnerability to threats (i.e., species exposure, sensitivity, and adaptive capacity). By doing this, we scientists and conservationists could better inform decision-makers about adequate conservation strategies. Alternative conservation strategies, such the use of surrogate species for conservation, should not be ruled out. But, more importantly, future conservation initiatives must be drawn up with a clearer and more specific objective to include overlooked species, adjust specific actions to address specific threats, and satisfy species conservation needs.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/plants14142184/s1>. Table S1: Reference of occurrence datasets retrieved from GBIF database. Table S2: Bioclimatic variables retrieved from CHELSA database and used in this study. Table S3: List of R packages used in this study. Table S4: Studies about desiccation-tolerant vascular plants in West Africa. Q1—Did the study discuss conservation needs of DT plants?; Q2—Did the study provide enough evidence that justifies the conservation needs of DT plants?; Q3—Did the study propose effective conservation strategies for DT plants?; Categories: I—Studies focusing on the entire community; II—studies focusing on specific community components; III—studies focusing on ecological processes and functioning. Table S5: Species presence (1) and absence (0) across 123 inselbergs in West Africa. Ap—*Afrotrilepis pilosa*, As—*Asplenium stuhlmannii*, Cy—*Craterostigma yaundense*, Mi—*Microchloa indica*, Ms—*Microdracoides squamosa*, Oa—*Oropetium aristatum*, Pd—*Pellaea doniana*, Ps—*Phymathosorus scolopendria*, Sf—*Sporobolus festivus*, Tm—*Tripogonella minimus*. Table S6: Species exposure to two anthropogenic drivers of biodiversity loss: quarrying and climate change. The evaluated species are *Asplenium stuhlmannii* (Aspleniaceae), *Phymathosorus scolopendria* (Polypodiaceae), *Pellaea doniana* (Pteridaceae), *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae), *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minimus*, and *Sporobolus festivus* (Poaceae), and *Craterostigma yaundense* (Linderniaceae). Table S7: Species exposure to quarrying when comparing unprotected and protected inselbergs. The evaluated species are *Asplenium stuhlmannii* (Aspleniaceae), *Phymathosorus scolopendria* (Polypodiaceae), *Pellaea doniana* (Pteridaceae), *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae), *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minimus*, and *Sporobolus festivus* (Poaceae), and *Craterostigma yaundense* (Linderniaceae). Table S8: Species exposure to climate change when comparing unprotected and protected inselbergs. The evaluated species are *Asplenium stuhlmannii* (Aspleniaceae), *Phymathosorus scolopendria* (Polypodiaceae), *Pellaea doniana* (Pteridaceae), *Afrotrilepis pilosa* and *Microdracoides squamosa* (Cyperaceae), *Microchloa indica*, *Oropetium aristatum*, *Tripogonella minimus*, and *Sporobolus festivus* (Poaceae), and *Craterostigma yaundense* (Linderniaceae).

**Author Contributions:** W.I.S. and L.B. contributed to conceptualization; methodology; formal analysis; data curation; writing—original draft preparation; and visualization. S.P. and E.L.B. contributed to supervision and made the data available. All authors contributed to writing—reviewing and editing the final draft. All authors have read and agreed to the published version of the manuscript.

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## Abbreviations

The following abbreviations are used in this manuscript:

|      |                                                |
|------|------------------------------------------------|
| DT   | Desiccation-tolerant                           |
| IUCN | International Union for Conservation of Nature |
| SSP  | shared socioeconomic pathway                   |

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